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TREE TEMPERATURES AND THERMOSTASY

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It is commonly assumed that, with minor variations, the temperature of the plant body is essentially that of the surroundings, or to be specific that the root system practically holds the temperature of the soil, while the stem temperature is that of the air. Stiles ('36) states, for example: "Any difference in temperature, however, between the plant and the medium in which it lives is generally very slight, and it has been stated that the temperature of growing shoots is not as a rule more than 0.3° C. above that of the surrounding atmosphere." Pfeffer ('06, Vol. 3, p. 381) says: "Hartig found, for instance, that the interior of a tree trunk sank to -13° C. during a winter when the air was frequently at -15° C. to -22° C. in spite of the upward flow of heat from the warmer roots." Although numerous more or less intermittent records of the temperatures in tree trunks have been made by use of thermometers, it has not been possible, until the invention of modern thermographs, to follow the temperatures, minute by minute, through long periods of time, as in the study to be reported upon here.

Variations of tree temperatures from those of the surrounding air have been noted from time to time. Elevated temperatures were believed to be caused by local, excessive respira-

tion or to slow cooling following periods of high air temperatures due to slow heat conduction of the tissues. Temperatures below those of the air have been assigned to the slow heat conduction of the tissues, or to the transpiration stream pulling cool water from the soil up through the stem. Mason ('25) described a partial thermostatic action in the growth center of the date palm which "is able to neutralize much of either cold or heat as the case may be, that has penetrated from without." This he attributed essentially to "the ascending sap current, with a temperature acquired from the soil from which it is drawn by the roots." Various investigators had previously noted occasions when tree temperatures were either above or below those of the air, but no regulation of tree temperatures except through insulation effects of the bark and the equalization action of soil temperature has been seriously considered. From the results to be reported here it will be evident that under certain environmental conditions there is a distinct thermostatic action in trees involving new concepts of physical conditions within them and resulting in significant benefit to them.

Apparatus and Methods

In planning this study the effort was to attain accuracy together with a minimum of artificial conditions. It was recognized that conduction of heat into and out of the organism by the apparatus might lead to serious error and that intermittent observations might miss important information. After an investigation of several of the chief types of recording instruments, a resistance thermometer was adopted as the most satisfactory. The apparatus, kept in operation for about four years, was an adaptation of a commercial instrument manufactured by the Brown Instrument Company and composed essentially of two main units, the recording instrument (fig. 1) and three sensitive resistance bulbs (fig. 2). The resistance wires of pure electrolytic nickel were enclosed in pyrex glass protective tubes. Although glass has some disadvantages, especially its relatively low rate of temperature conduction, its characteristics seemed less likely to cause error than those

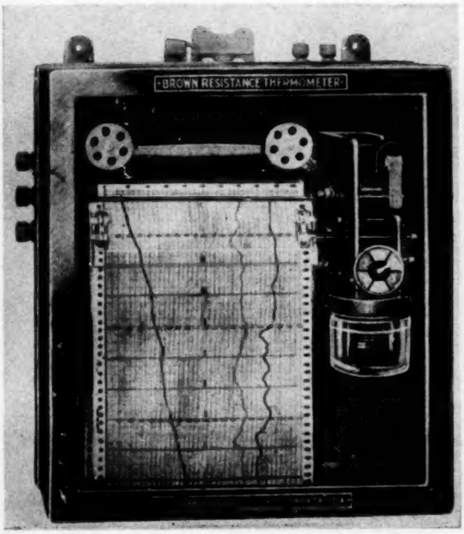

Fig. 1

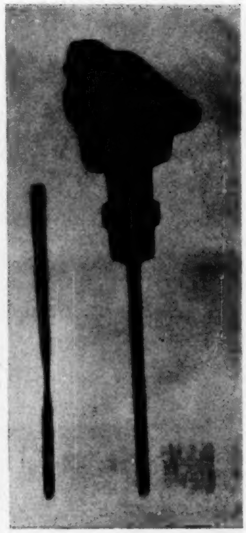

Fig. 2

of other materials. As a means of reducing so far as possible any conduction of heat or cold either from or toward the selected tissue and to give added mechanical protection, a celeron fiber tube encased the glass down to the sensitive elements. A three-wire cable connected each of the bulbs with the automatic recorder.

The recording instrument is described briefly as follows by the manufacturers:

"It consists of a Wheatstone bridge with two ratio arms of equal resistance, a third arm consisting of a resistor having electrical resistance equal to that of the bulb at maximum temperature, and the fourth arm a resistor having resistance equal to that of the bulb at minimum temperature; a switch permitting transposition of the bulb into the bridge circuit in place of the latter resistor; a galvanometer and storage battery, with standardizing rheostat, being connected to the bridge at the proper points; the galvanometer scale being suitably calibrated in temperature units."

This is a completely automatic, electrically driven apparatus with synchronized clock and a three-record chart in different colors having a temperature range of –35° C. to +40° C. The chart moved at the rate of ¼ inch an hour, and a record of each bulb was made every 3 minutes with a 20-second depression of the needle. Small differences of temperature may most readily be recorded over a range limited only by the recording device; and several different records, covering long periods of time, may be kept simultaneously on the same sheet of paper for direct comparison.

A cottonwood tree *(Populus deltoides* Marsh.), with a trunk about 10 inches in diameter at 30 feet from the ground, where the bulbs were inserted, was selected for study. In setting up the apparatus the three bulbs were distributed as follows: One was inserted with its sensitive element at the center of the tree. The second bulb was placed on the southeast side of the tree, as near the cambium layer as possible, by boring a hole from the opposite side of the trunk. Hence the tissues external to the bulb were left intact, and necessary mechanical support for the bulb was obtained. Both holes were bored to the diameter of the celeron tube to obtain a tight fit. The tight-fitting apparatus was undisturbed for the period of the experiment, so

that its physical continuity with the tissues of the plant was not broken. Much of the success in obtaining the detailed and continuous record described later may be ascribed to this fact. The third bulb, which recorded the air temperature, was placed in a small cage built in imitation of the U. S. Weather Bureau shelters, to screen it from direct sunlight and rain. During the growing season all the bulbs were shaded by the tree foliage.

The immediate problem was to determine accurately the fluctuations of the tree temperatures in relation to those of the air and to discover any indication of a control of the temperature by the tree itself.

It was possible to read readily from the record-charts 0.25-degree changes of temperature and to compare almost minute for minute the temperatures of the three bulbs. Photographic reproductions of many of the original graph-records made during the 4-year study are cited by date in the body of the text and may be identified thereby. The diagram in fig. 3, which is an exact copy of a typical medium temperature record, will help to understand the general principles followed in interpreting the graphs reproduced at the end of the paper.

GENERAL PRINCIPLES FOR READING THE CHARTS

1. The usual record for a 24-hour period shows (fig. 3) the air temperature beginning to rise at from 5 to 8 a. m., reaching a maximum between 1 and 5 p. m., followed by a decline in the late afternoon and night. Commonly the air-temperature line (A) crosses the tree-temperature lines (H and C) during the early morning rise of the air temperature and again in the afternoon with its decline. At these intersection points (W, X, Y, and Z) the air temperature is momentarily the same as that of the tree center (W or Y) or cambium (X or Z). Many modifications of this daily record appear, as will be seen in the graphs, and even complete inversions of the air temperature may occasionally take place when it increases during the night or decreases during the day. Nevertheless, this fundamental type must constantly be borne in mind when these records are being examined.

2. Air-temperature increases, before the morning intersections of the temperature lines, cannot *raise* the tree temperatures because the air temperature is *below* those of the tree.

3. Air-temperature decreases, before the afternoon intersections of the temperature lines, cannot *lower* the tree temperatures because the air temperature is still *above* those of the tree.

Fig. 3. Typical record of the three tree temperatures. The lines A (air), H (tree center) and C (cambium) are the first portions of the temperature records for the 24-hour period, 7 a. m. to 7 a. m. W and X are the a. m. intersections of A with H and C respectively, and Y and Z the corresponding intersections made during the p. m. decline in temperature. Later, W, X, Y and Z are denominated "iso-thermal nodes." In the original graph-records the vertical lines represent 0.5° C. and the horizontal lines, reading from bottom to top, 1-hour intervals from a. m. to p. m. The numbers on the horizontal lines of the graph-records are to be disregarded, but the temperature lines are correctly numbered. In the graph-records and in this figure, therefore, temperature increases from left to right and time advances upward.

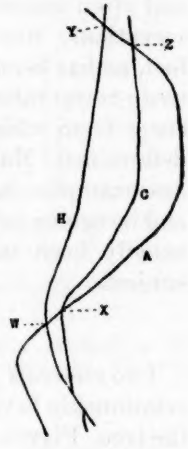

Fig. 3

4. However, such an increase before the intersections W and X in the morning, or a decrease before the intersections Y and Z in the afternoon, does *slow down the rate* of the temperature changes in the tree and hence will prolong the time between the minimum air temperature and the minimum tree temperatures in the morning and between the maximum air temperature and the maximum tree temperatures in the afternoon respectively.

5. From 2 and 3 above, it will be evident that, in calculating the direct effect of air-temperature change upon the tree temperatures, only the number of degrees after the morning intersections and the afternoon intersections respectively should be counted.

6. The same intersections must be used as the basic points in calculating the degree-hours as described later.

7. As long as the cambium temperature is appreciably above that of the center the latter continues to rise regardless of whether the air temperature is rising or falling.

8. Tabulations of maxima and minima or of mean temperatures have not usually been presented, although heretofore most of the published data on tree temperatures have been given in this form. Such tabulations are usually inadequate and often inaccurate due to infrequent or arbitrarily timed observations. Much of the value of the present records would be lost, as has been true of former published data, by the use of mean temperatures, since averages iron out individual differences from which, in studies of this type, principles may be determined. Maxima and minima, as can be seen from numerous examples in these records, very often cover considerable and irregular periods of time and are not merely points, as has usually been tacitly accepted in former studies upon this subject.

"DEGREE-HOURS"

Two methods have been adopted to indicate the quantitative relationship between rise in temperature of the air and that of the tree. Figure 4 is a tracing of the lower portion of a typical graph-record in which LM represents the hour at which the air-temperature line (T_A) makes an intersection in the morning with the tree-center temperature line (T_H) during the daily rise in T_A. The intersection point is A and is referred to as "T_A min." in the discussion and tables. DB represents the hour at which T_A reaches its maximum, and B is "T_A max." E is the point at which T_H begins to rise and is "T_H min." AD is the temperature line on the chart through A. XF is the temperature line on the chart through E. CF equals XE; and FG represents the hour-line through F. G is taken as "T_H max." The reasons for adopting these limitations have been partly indicated in the preceding section, and will be given in detail in further discussions. If the increases in temperatures were perfectly steady and T_A and T_H therefore straight lines, DB and FG would correctly indicate the increases and the ratio

DB/FG would be a measure of the net effect of air-temperature rise upon tree-temperature rise. For certain purposes it has seemed satisfactory to use this ratio as given in some of the following tables. However, since T_A and T_H usually depart considerably from the straight line a more accurate method of estimation was adopted. Any area on the chart, as for example ABD or EFG, bounded by the temperature record line and any given temperature base line and within any given time limits, may be rather accurately determined by counting the small rectangular spaces of the graph paper. The number of these spaces, divided by two, because each space represents 0.5° C., gives the "degree-hours" for this area. The ratio ABD/EFG is taken as a measure of the total net effect of atmospheric temperature change upon the temperature change in the tree over the given period of time.

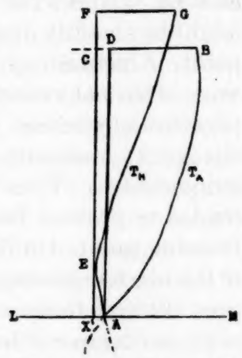

Fig. 4. Method of determining the "degree-hours."

General Results

As would be expected, there is always a "time-lag" between temperatures of the tree and those of the air. This occurs in a temperature change, as well as in the attaining of a maximum or of a minimum, and is greatest at the center of the tree. The length of this "lag" period is extremely variable, depending upon the interrelations of a number of factors. Since the physical conditions in the tree and the environmental factors are so variable, the results of the investigation are best considered under three headings: (1) "low" temperatures, from about 10° C. downward; (2) "high" temperatures, from about 30° C. upward; and (3) "medium" temperatures, in the intermediate zone. The limits of these three temperatures ranges are only very broadly placed, and under certain conditions the "medium" range extends above or below the limits indicated. The

generalizations stated below are supported by selected "case studies" given in detail later.

LOW TEMPERATURES

One of the outstanding tendencies during the colder portions of the year was for the tree temperatures to remain steadily at 0 to –1.5° C. for many hours while the air temperatures might be steadily dropping below freezing or rising above that point. Fluctuations between day and night air temperatures were often not reflected at all or only slightly in the tree temperatures, whereas a corresponding number of degrees of change at moderate temperatures directly affected the tree temperatures. Thus there was exhibited a buffer action which tended to prevent frequent changes in temperature across the freezing point. On the other hand, after 24–48 hours or more, if the air temperature continued to change in the same direction, the tree temperatures began to follow the general course of the air temperature and eventually approximated any steadily maintained air temperature.

HIGH TEMPERATURES

During the summer of 1934, and especially the latter half of the month of July, high temperatures and low atmospheric humidities provided an exceptional opportunity to study the relationships of tree temperatures to high air temperatures in the absence of many of the usually complicating factors.

When the air temperature rose to above 35° C. and there was a low relative humidity, the center temperature of the tree dropped contemporaneously over a variable period of time until an equilibrium was reached, after which it began to rise with the drop in the air temperature. On the hottest days, when the air temperature was 42.5° C., the center temperature was 27 to 27.5° cooler. On other days the center was 22 to 26° cooler than the air with a low varying from 15 to 17° C. If, during the day, the air temperature rose and fell more than once, the center temperature of the tree changed in the opposite directions immediately. The rate and amount of change were less than

those of the air but were in a definite ratio to the air changes. Frequently during July 18–25 a sudden rise or fall of even 1.5° in the air temperature produced an immediate drop or rise respectively in the center temperature of 0.5° or more. The cambium temperature varied much less sharply than that of the center and air. It tended to rise in the morning with that of the air, but later attained an equilibrium between the air and the colder center temperatures. A subsequent slow rise, usually culminating about 5 hours after the beginning of the drop in the air temperature, varied slightly with the speed of change in the center and air temperatures. Thus, on July 19, 1934, at 4 p. m. when the air temperature (39.5° C.) began to drop, the center temperature was 17° C. while at 7 a. m. the next day it was 22° C. Here was a rise of 5° in 15 hours in the tree center occurring simultaneously with a drop in the air temperature of 13°. The cambium meantime had changed only from 30.5 to 32.0° C. On July 20, from 5:30 p. m. to 2 a. m. the center temperature changed from 16.5 to 21° C. and the cambium rose from 31.5° to only 32.5° C. in 5.5 hours. The cambium temperature usually rose with the rise of the center temperature and against the drop in the air temperature, although concurrent with a rapid rise in air temperature there was at times a temperature increase in the cambium.

From these observations it is clear that the temperature of the cambium region is a resultant of the cooling effect of the tree temperature acting against the absorption of heat from without. During the early morning of July 14 the rapid drop in the air temperature carried it below the two tree temperatures. During the same period the influence of the temperature of the air on that of the cambium is shown by the decline of the latter. As the temperature of the air began to climb, however, and that of the center began its daily drop, the cambium temperature tended at first to follow the direction of the air but finally took the downward course of the center temperature. The effectiveness of this thermostatic action is seen in the records, for example, of July 21 and 22. Early in the morning the cambium temperature began to rise with, and to follow fairly

closely, the air temperature until the cooling effect of the center definitely pulled it down again in about three hours, even when the air temperature was still rapidly rising. At other seasons of the year the cambium was often at the same temperature as that of the air.

It appears that there is only one adequate cause of the almost instantaneous reduction of temperature of the center of the tree during the periods of high temperature increases. High air temperatures, both directly and through effecting a rapid decrease in relative humidity, set up an increased transpiration which caused a certain water deficit in the tissues of the tree. This in turn resulted in a rapid interior vaporization of water which absorbed large amounts of heat, thus cooling the tissues.

MEDIUM TEMPERATURES

At moderate, steady temperatures, associated with other steady climatic conditions, the two temperatures of the tree, which ran close to those of the air, were almost identical, and their rise usually began very soon after that of the air. However, the beginning of the decline in the cambial temperature was usually delayed 3–4 hours after the initiation of the fall in the air temperature, while that of the tree center was frequently delayed 1 to 2 hours longer, during which time the latter even continued to rise. When there were gradual changes in the air temperature the changes in tree temperature kept pace, with only slight lag. When there was a more rapid and sharper change in the air temperature, as frequently in passing from night to day, the tree temperatures showed much less change. Thus differences between day and night air temperatures of about 16° were reflected in corresponding tree temperatures by differences of only 2.5 to 3.5° (table I).

At times, even under moderate conditions, as on July 15, 1932, increases in air temperatures resulted in slight, but definite, slow reduction in the center temperature, thus exhibiting the thermostatic tendency; and at other times the cooling action is evidenced by an unusual wide spread between the air-

TABLE I

Date 1934	Air temp.	Time	Cambium temp.	Time	Center temp.	Time
May 27–28	High 27	12 m.	20.5	8 p. m.	19.5	9 p. m.
	Low 11	4–5 a. m.	17.0	7 a. m.	16.5	8–9 a. m.
	Diff. 16		3.5		3.0	
28–29	High 29.5	12 m.–4 p. m.	22.0	8–10 p. m.	20.5	10–12 p. m.
	Low 13.0	5 a. m.	18.5	7 a. m.	18.0	8 a. m.
	Diff. 16.5		3.5		2.5	

and the tree-temperature lines. However, at moderate temperatures this tendency was often obscured by other factors.

When the air temperature was between 20 and 30° C. the cambial temperature kept close to it. During periods of slight, slow changes of air temperatures, cambial temperatures were often maintained 0.5 to 1.5° above those of the tree center, regardless of whether the air temperature was above or below that of the tree center. This might seem to indicate a tendency for the cambium region to maintain its own temperature somewhat independent of the influence of the air and center temperatures.

We may conclude that, at or near the critical temperatures of freezing and of heat injury to protoplasm, living cells of the tree trunk are partially protected through special physical adjustments. These physical adjustments, during high temperature periods, are dependent upon the excessive transpiration often induced by heat. Hence during such periods not associated with excessive transpiration the tree might not exhibit the physical adjustments indicated above; and under high transpirational conditions, induced by other factors than excessive temperatures, an increased internal vaporization might be induced.

Detailed Study of Specific Periods

LOW TEMPERATURES

The temperature of the cambium layer is mainly influenced by that of the air, but it is evident that in the changing climatic

conditions of the area in which these studies were made the cambium layer and the air are seldom at the same temperature. When the temperature of the air is on the decline that of the tree center is usually higher than that of the air, while with the air temperature rising the tree center is soon colder than the air. This relatively warm or cold center slows down the upward and the downward tendencies of the cambium temperature in response to the rise and fall of the air temperature respectively. This was particularly evident when the air temperature line crossed the zero temperature line in continuous upward or downward swings following a steady period below or above zero. After an adjustment in the tree had been made at about the zero line the temperatures followed the direction of the air temperature with relatively slight lag in time but did not usually reach the extremes of the air temperature until the latter had become steady for several hours. These conditions, as well as the usual buffering action at the freezing point, are well illustrated by the following typical examples.

1. The tendency for the temperatures of the tree to follow closely those of the air after the tree had become adjusted to freezing weather is shown by the cold spell in the early part of March, 1932. From March 8 to 12, the tree temperatures closely paralleled those of the air which varied most of the time from –3.0 to –10.0° C. Also, during the night of March 12–13, 1932, the air temperature dropped from –3.5° to –9.5° C., and in an essentially coincidental drop the tree-center temperature reached –8.5° C. an hour later. This period had been preceded by 36 hours of sub-freezing temperatures in the tree, the cambium having attained a minimum of –4.0° C. and the center –4.75° C.

The following specific examples illustrate well the usual buffering action at the zero line, by which the tree temperatures are held steadily at or close to zero for many hours or by which the cooling of the tree tissues is considerably slowed down.

2. At 11:00 p. m., November 14, 1932, the air temperature dropped from 14.0 to 9.0° C. in 0.5 hour, followed by a slower almost uniform drop to –8.0° C. at 6:30 a. m., November 16, or

a total drop of 22.0° in about 32 hours. The cambium and center lines began their drops in 0.5 and 1.5 hours respectively, and after 2.5 hours they were essentially superimposed. The center temperature reached zero at about 10:00 p. m., November 15, 23 hours after the beginning of the cold spell and 11 hours after the air temperature crossed the zero line. It then very slowly dropped in 8 hours, November 15–16, approximately 1.0° more, while the air temperature dropped from –5.0 to –8.0° C., giving a ratio of air temperature drop to tree temperature drop of 3:1. During the night of November 17 and 18 the air temperature dropped from –0.25 to –6.0° C. in 10 hours, while the tree center dropped only from 0.25 to 0.50° C. in that time. This gives a ratio of 23:1. On November 19 a 4.0° air-temperature drop resulted in a 0.5° drop in the tree center, or a ratio of 8:1. From 9:00 p. m., November 15, for more than 6.5 days, the cambium temperature was about a degree higher than that of the center, while neither showed more than a slight variation up or down. Meantime, the air temperature was mainly somewhat below zero, but with short, upward turns to about +5.0° C. on November 17 and 18, and 16.0° on November 20. Finally, on November 22, following a 12-hour rise in air temperature to about 8.0–10.0° C., the cambium, at 3:00 p. m., and the center, at 10:00 p. m., began their periods of rise. This case history demonstrates the tendency for the tree temperatures to remain at about zero even when the air temperature alternated from –8.0 to +16.0° C. It also shows, under an essentially constant zero tree temperature, the tendency for the temperature of the cambium to remain slightly higher than that of the center, even when that of the air is mainly below both tree temperatures.

3. At about 4:30 p. m., December 6, 1932, a sharp drop in air temperature from about 20.0 to 5.0° C., followed by a slower decline to a minimum of –10.00° C., initiated an 11-day period of sub-zero weather, mostly between –5.00° and –10.00° C. During the first 28 hours after the center temperature reached zero the cambium remained about 0.5° above the center temperature, with the cambium attaining and holding a temperature of

–0.5° C. Then the cambium line gradually crossed the center line at about –1.25° C., and for more than 24 hours the cambium temperature remained about 0.5° lower than the center, while both temperatures were dropping to approximately –5.0° C. This case illustrates the usual tendency, under these conditions, for the cambium to hold a temperature during day and night slightly higher than that of the center while both remained at about zero. It shows also the tendency for the cambium subsequently to respond somewhat more rapidly than the center, as it does at more moderate temperatures, to the further changes in the air temperature. During the long cold spell following the above initial drop in temperature the air temperature, on December 7 and 8, fell from –5.0° to –9.75° C., while the tree center fell from 0.0° to –1.25° C., a ratio of 3.8 :1. During the next two days a drop in air temperature from –3.5 to –10.00° C. brought about a drop in the tree center from –1.0 to –1.75° C., a ratio of 8.6 :1, while from December 9 to 10 an air-temperature drop from –7.5 to –9.5° C. caused a tree-center drop from –3.0 to –5.00° C., a ratio of 1 :1. This shows that after the tree had been at a sub-freezing temperature for an extended period, in this case approximately 45 hours, a degree of air-temperature reduction was much more effective in lowering the tree temperature than when the tree had been only for a short time at the sub-zero temperature. This greater effectiveness of a change after a long period of sub-zero air temperatures is shown in a further drop in temperature beginning about 7 p. m., on December 11, 1932. In 12 hours the air temperature dropped from –2.75° to –15.50° C. Correspondingly the tree center dropped from –3.75° to –11.25° C., a total of 7.50°, giving a ratio of 1.7 :1.0. The tree tissues had constantly been at sub-zero temperatures from the morning of December 8.

4. From December 19 to 22, 1932, the tree center held steadily at –0.5° to –1.5° C., with the cambium usually about 1 degree higher, although at one time the air temperature was above zero for more than 24 hours with a maximum at 11.5° C. Finally, on December 22 to 23, a rise in air temperature to +14.0° C. caused a slow rise in the tree temperatures almost to

that of the air, with the cambium temperature at the time of the air maximum 1 or 2° higher than that of the center. On the downward swings of the curves between December 7 and 22 the cambium- and center-temperature lines soon (3–4 hrs.) became superimposed, when the air temperature change was 5–8° C. in 12 hours; or the cambium assumed a temperature slightly below that of the center when more rapid or extensive depressions of the air temperature occurred.

5. From about 3:30 p. m., March 9, 1934, for 60 hours there was a zero to sub-zero air temperature reaching –12.0° C. in a continuous drop from zero in 14 hours. Twice it rose to +1.5° C. for an hour or less, but otherwise it was mostly zero to –4.5° C. During all of this period the center tree temperatures were from –1.50° to –1.75° C., and the cambium about –0.5° C., except at the coldest period when it was –1.0° C. For the total period the ratio of T_A drop to T_H drop was 4.7:1.

6. The period of 34 hours, from March 18 to 19, 1934, with an air temperature minimum of –10.25° C., gave rise to a steady tree-center temperature of –0.5 to –2.0° C. for about 35 hours, beginning about 8 p. m., on March 18. During the initial change T_A dropped from 16.0° to –4.5° C., while T_H dropped from 16.5° to 1.0°, or a ratio of 1.3:1. During the second significant lowering of temperature T_A dropped from –1.0 to –9.5° C., while T_H dropped from 0.25° to –2.0° C., or a ratio of 3.7:1. In this case, approximately three times as many degrees of change in air temperature were necessary to cause one degree change in the tree temperature at or immediatly below zero as above it.

7. On March 5, 1932, at 3:30 a. m., there was a sharp drop in air temperature from 5.50 to –11.25° C., in about 28 hours. The tree-center temperature began to drop about 1.5 hours later, and the cambium in 0.5 hour. Thus there was a "lag" of only 1.5 hours in the beginning of the response of the center temperature to the change in air temperature. At this season of the year there is little or no heat used in the vaporization of water in the tissues, and at this time of day no direct insolation to complicate the situation. At temperatures above 0.0° C. the complications of freezing action are also absent. This is ap-

parently a good example of "lag," due simply to the rate of heat transfer through the tissues. For over 56 hours the air temperature remained at -4.0 to -11.5° C., and for about 28 hours from the time that the tree temperatures reached 0.0° C. they held between that point and -1.25° C. For about 10 hours after the tree temperatures had reached zero they declined further only when the air temperature decreased again. For example, when the air temperature remained at -7.00 to -7.25° C. for 6.5 hours (7:30 p. m. to 2:00 a. m.), the tree center remained at -1.0° about 8 hours. Following the further drop in air temperature, the tree temperature began to drop slightly, and minor fluctuations continued in accord with those of the air. There was then a period of several hours of adjustment, near the zero line. Later, when the air temperature remained steadily at -11.0° C. and even after it began to rise, the tree temperature continued to fall for at least 6 hours. In this period the tree-temperature reaction was similar to that under moderate temperatures. During the first decline in air temperature the tree center dropped 6.25°, while the air temperature made its drop of 16.75°. This gave a ratio of T_A to T_H of 2.6:1. During the second period of decline the ratio for the last 12 hours was about 1.3:1, which indicates that the zero-line adjustment had almost been completed in the preceding 32 hours.

8. On January 29, 1932, a sub-freezing period of 3 days with minima at -11.5 and -9.0° C. began. A steady drop in air temperature from 5.0 to -11.5° C. carried the tree center from 9.5 to 1.0° C. The ratio for this period above zero in the tree was 1.05:1. While the tree temperature was crossing the zero line from 1.0 to -1.50° C. the air temperature dropped from -4.0 to -11.5° C., which gave a ratio of T_A change to T_H change of 3:1. During this time the tree temperatures remained steadily at 0.0 to -2.0° C. and continued so 24 hours longer in spite of almost continuous air temperature of 5.0° C. during this latter period. The cambium temperature then began a slow rise to a maximum of 2.5° C., with an air maximum of 9.5° C. Meanwhile the center temperature remained steadily at -1.0° C. for another 4 days despite air temperatures for several hours from 5.0 to 13.0° C. on the last of these days.

9. The tendency for the tree temperatures to hold at or near 0.0° C. during frequent and sometimes rather extensive upward and downward changes of air temperature is further shown in the record of November and December, 1932. For example, from November 16 to 22 the tree temperature was essentially unchanged, while the air temperature shifted from -7.0° C. at night to +10.0° and once to +16.0° C. in the daytime. During this period the cambium temperature continued almost uniformly at +0.5° C., and the center at about -0.5° C.

10. From noon, January 12 to midnight, January 13, 1931, the center temperature remained at 0.0 to -0.5° C., and then slowly fell to -3.0° C. at noon the next day. It rose again in 12 hours to -1.0° C., and then for 3.5 days remained at -1.0 to 0.0° C. in spite of continuous air temperatures of 13.0 to 6.0° C. In this and two succeeding cases there is especially demonstrated the slow reaction of the tree temperatures at the zero line when the air temperature passes above zero after having been for some time below the freezing point.

11. Following the sub-zero period ending February 28, 1934, the air temperature rose and remained above zero almost all of the time for 80 hours, for 68 hours varying from about +3.5 to +10.0° C. During the entire period the center temperature held steadily at -1.5 to -0.5° C. and finally zero. The cambium stood at zero for 44 hours, with a gradual rise above that point for the rest of the time.

12. That the tree resisted temperature change when it had been at a steady sub-freezing temperature was shown on March 12, 1934. An air-temperature rise to 18.0° C. gave a total of 90 "degree-hours," while only in the latter part of this period the tree center had a 3 "degree-hour" rise, or a ratio of 30:1. This contrasts sharply with the degree-hour ratios for periods of moderate temperatures as shown elsewhere.

13. About 9 a. m., January 28, 1934, the air temperature dropped steadily from about 10.0 to -16.5° C., a total of 26.5° in about 24 hours. When the air temperature was -14.0° C., the superimposed tree temperature lines were carried across the zero line without any apparent retardation in rate of fall. Following a rise of a few degrees there was a second period of de-

cline in temperature, during which that of the air was 7.75° C., and of the tree center 5.0° C. This shows a ratio of 1.55:1. During the first period of decline the tree center dropped 12.0° in response to the 26.5° of the air, or a ratio of 2.2:1. Hence, although no visual retardation occurred at the zero line it is evident that during the first period a 2.2° change in air temperature was necessary to cause a 1° change in the tree, while during the entire second period after the internal adjustments had been made, only 1.55° of change in the air temperature was needed to cause 1° change in the tree temperature. This latter value agrees very well with the cases cited for periods of temperature change after the zero line adjustments had mainly been made. During the second period a change in speed of drop in the tree temperature occurred at about 10 p. m., January 29, although no change in speed for the air-temperature drop is evident. From that point to the end of the period the ratio between the two temperature declines was 1:1. Since this occurred during the night when there were no complicating conditions, it demonstrates that the theoretical value for this relationship may be actually reached when there are no restraining influences. The attainment of this value also emphasized clearly the retarding influence of the zero line on the decline in tree temperatures, during the first period, when the ratio was 2.2:1.

HIGH TEMPERATURES

The marked, thermostatic response of tree temperatures to changes in air temperature during periods of extreme heat was first noted in the records for the latter portion of July, 1934, although records of other years give the same indications in a less extreme form. The graph-records for the period of July 15 to 26 reveal the principal fact that with every morning advance in air temperature there was usually an immediate decrease in the tree temperatures and with each afternoon decrease in air temperature there was a corresponding immediate increase in the tree temperatures. For the whole period, table III lists the data which show that for 2.48° rise in air temperature there was a 1.00° lowering of the temperature of

the tree center and for each 2.83° drop in the air temperature there was a 1.00° rise in the tree-center temperature. It should be noted that, in view of the cause of this phenomenon as indicated later, these ratios represent maximum values, since a more complete insulation would have more successfully prevented heat interchange with the environment, and it would have taken a smaller change in air temperature to effect a degree change in the tree temperature. Also it should be noted, as indicated in table II, that throughout this period the tree temperatures averaged much below those of the air, and that, in contrast to periods of moderate temperatures they were seldom *directly* influenced by fluctuations in the external temperature.

TABLE II

MAXIMUM EXTREMES

1934 July	Tree center T_H min.	Diff. T_A max. and T_H min.	Air T_A max.	Diff. T_A max. and T_C min.	Cambium T_C min.
20	16.5° C.	26.0°	42.5° C.	11.0°	31.5 to 32.5° C.
21	16.5° C.	23.5°	40.0° C.	9.0°	31.0 to 32.0° C.
22	16.0° C.	23.5°	39.5° C.	8.5°	31.0 to 32.0° C.
23	15.0° C.	27.5°	42.5° C.	11.0°	31.5 to 32.5° C.
24	15.0° C.	27.5°	42.5° C.	10.5°	32.0 to 33.0° C.
25	15.5° C.	27.0°	42.5° C.	10.5°	32.0 to 32.5° C.

During the day throughout this period the line registering the cambium temperatures was always between the other two lines and usually about 10° below that of the air temperature. This shows that some influence antagonistic to the heating action of the atmospheric temperature was at work. The chart indicates clearly that the cold central zone provided this influence. Radiation of heat from the cambium zone inward kept this zone from attaining the temperature of the ambient air and its temperature therefore was a resultant of the heat from without and the cold from within. Had this tissue been located midway between the center and the outside it would be expected that its temperature would have approximated the average of the air and center temperatures. However, when, as on July

15, 18, and 20–25, the maximum air temperature of 38–42° C. continued for from 4 to 6 hours the cambium-layer temperature would be expected to rise rapidly due to continued absorption of heat from the outside. Nevertheless, during this period, because of the counter cooling action of the central cold zone, it usually remained almost constant, or with only a slight increase. During certain other portions of the year in such a period of uniform air temperature when the various other factors were steady the cambium temperature closely approximated that of the air.

Two main factors thus were concerned in determining the temperature of the tree at this time of year. The first was the flow of heat from high to low, that is during the day from the environment inward; and the second was the *active* withdrawal of heat from the tree tissues. This latter action, as amply demonstrated in the records, increased and decreased directly with the increasing and decreasing air temperature, and its cause must then be associated with some reaction of the plant to temperature changes. The relative intensity of these two factors determined the exact temperature attained in the tree. With an increase in the air temperature the cooling action increased faster than the transfer of heat inward from the environment, while during a decrease in the air temperature the transfer of heat inward exceeded the cooling action. Early in the day the cambium attained an approximate balance between the two factors and later a balance was also reached in the tree center, resulting in a longer or shorter period of an approximately steady, low temperature. The application of these principles accounts for the details of a typical record such as that of the following.

From 9:00 p. m., July 13, 1934, the usual steady decline in air temperature continued until 1:30 a. m. on July 14, when there was a sharp drop of 9.5° in the air temperature which ended at 6:00 a. m. Meanwhile the center temperature, coincident with the slow decline in air temperature, continued its slow rise of the night period until 1:30 a. m., at the rate of 1.25° in 4.5 hours. From 1:30 a. m. until about 4:15 a. m. it rose 1.25°, thus

increasing the rate to 1.25° C. in 2.75 hours coincident with that of air-temperature decline. This immediate, inverse relationship is also visually shown by the fact that at exactly 1:30 a. m., when the air temperature began its sharp decline, there was a very slight but definite *upward* movement in the record of the tree-center temperature. From 4:30 to 6:00 a. m. the center temperature remained steadily at 24.75° C., when it began its drop in response to the rise in the air temperature. This record of the center temperature, like that of the cambium, indicates the compound character of the tree temperature. At first the heat added to the system, including the flow inward from the outer tissues, exceeded that absorbed through the internal cooling, and the tree temperature rose. From 4:30 a. m., for 2.75 hours, the transfer of heat inward and the cooling effect balanced one another, causing the leveling of the center-temperature line. At 6:00 a. m. the cooling action began to increase, coincidental with the beginning of the rise in air temperature, and became greater than the inward flow of heat. Therefore the center-temperature line shows the beginning of the daily decline which culminated at about 3:45 p. m. and which caused a drop from 24.75° to 18.00° C., or a total decline of 6.75°, while the air temperature was rising from 22.00 to 36.00° C., or a total of 14°. From 3.45 p. m. until about 6:15 p. m. slight but definite fluctuations in the air temperature were inversely reflected in the center temperature. From then on the regular nightly drop in the air temperature was reflected in the rise of temperature in the center of the tree.

During the next 12 days there were similar conditions, often in intensified form, which may be seen in the graph-records and in table III. The tree-center maximum (T_H max.) and the air-temperature minimum (T_A min.) usually occurred at the same time in the early morning, and the tree-center minimum (T_H min.) and the air-temperature maximum (T_A max.) at the same time in the afternoon. However, the maxima and minima often covered considerable periods of time, and for tabulation purposes it was necessary to select some certain point in each of these periods. Because of the instantaneous response of the

tree to changes during the high-temperature period the point of beginning of the air-temperature rise was assumed to mark the point in the tree-temperature maximum when the morning air-temperature rise began to influence the tree temperature. This point then was used as T_H max. and T_A min. The other maximum and minimum points were selected by the application of the same general principle. From tables III and IV it can be

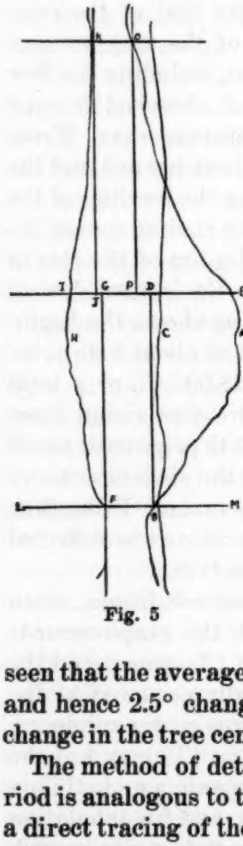

Fig. 5

Fig. 5. Demonstrating method of calculating "degree-hours" for high-temperature period.
BAO is the T_A line; FHK the T_H line; C, the T_C line; LM, the 7 a. m. line; IE, the 3:15 p. m. line, and KO at 5:15 a. m., July 21. The position of IE was fixed by the beginning of the decline in BAO. BAED is taken as the area representing the total heat in "degree-hours" during the air-temperature rise, and FHIG the corresponding number of "degree-hours" of temperature decrease at the tree center. Area PEO represents the total "degree-hour" decline in air temperature to the 5:15 a. m. line, and JIK the corresponding "degree-hours" of temperature rise at the tree center.

seen that the average ratio T_A change/ T_H change was about 2.5 and hence 2.5° change in air temperature caused 1.0° reverse change in the tree center.

The method of determining the "degree-hours" for this period is analogous to that in fig. 4, and is shown in fig. 5, which is a direct tracing of the record for July 20, 1934.

There are two possible explanations of the type of curve found in the record throughout most of July, 1934. The alter-

nating upward and downward movements of the lines might be due to an essentially regular "lag" period of twelve hours, by which the low tree temperatures of one daylight period

TABLE III

COMPARISON OF INFLUENCE OF RISE AND FALL OF AIR TEMPERATURE ON TREE TEMPERATURE

(a) 1934 July	(b) T_H max.*	(c) T_H min.†	(d) T_H change	(e) T_A min.#	(f) T_A max.§	(g) T_A change
Period of air-temperature rise						
14	23.75**	18.25	5.50	23.75**	34.75	11.00
15	22.00	18.25	3.75	25.75	38.50	12.75
16	23.25	19.50	3.75	26.00	37.50	11.50
17	21.75	17.75	4.00	22.75	32.75	10.00
18‡	21.00	15.75	5.25	25.75	37.50	11.75
19	21.50	17.25	4.25	26.75	38.75	12.00
20	22.25	17.00	5.25	28.75	42.00	13.25
21	21.50	17.25	4.25	27.25	39.25	12.00
22	21.50	17.50	4.00	27.25	38.50	11.25
23	21.50	14.75‖	6.75	25.00	36.50	11.50
24	21.50	15.00	6.50	29.00	42.00	13.00
25	20.50	16.25	4.25	29.50	41.50	12.00
26	20.00	19.00	1.00	27.25	30.25	3.00
		Total	58.50			145.00##
Period of air-temperature drop						
14	22.50¶	18.50	4.00	27.25††¶	37.00	9.75
15	23.75	19.25	4.50	27.50	39.00	11.50
16	21.50‖	19.50	2.00	27.50	37.50	10.00
17	21.25	19.00	2.25	26.75	32.00	5.25
18	21.75	15.25	6.50	26.50	39.25	12.75
19	22.25	18.00	4.25	28.75	39.50	10.75
20	21.25	17.25	4.00	29.50	41.50	12.00
21	21.50	17.50	4.00	29.50	40.00	10.50
22	21.75	17.25	4.50	25.50	38.75	13.25
23	21.25	18.25	3.00	32.75	41.75	9.00
24	20.75	16.00	4.75	29.50	42.25	12.75
25	19.50	16.50	3.00	33.00	42.00	9.00
26	18.00	17.00	1.00	30.00	33.25	3.25
		Total	47.75			129.75‡‡

* T_H max. taken at the same time as the end of the T_A min.
† T_H min. taken at the same time as the first point in the T_A max.
# T_A min. taken at the last low point before the rapid rise in the air temperature.
§ T_A max. taken at the first high point reached by the air temperature in the a. m. rise.
** T_H max. and T_A min. taken at a. m. intersection of T_A with T_H.
‡ Subsequent small changes in air temperature and inverse changes in tree temperature.
‖ 7:30 p. m.
†† T_A min. (for "Temperature drop") taken at the beginning of the steady high temperature of the tree.
¶ T_H max. and T_A min. taken at the first point in the T_H line at which it reached essentially a steady temperature, if not at the absolute T_A min.
T_A/T_H = 145.00/58.50 = 2.47:1.
‡‡ T_A/T_H = 129.75/47.75 = 2.71:1.

TABLE IV

HIGH-TEMPERATURE PERIOD. RATIO BETWEEN AIR-TEMPERATURE CHANGE AND TREE-CENTER TEMPERATURE CHANGE IN "DEGREE-HOURS." THE DIVIDING LINE BETWEEN "UP" AND "DOWN" (E.G. ON JULY 18 AT 3:45 P. M.) TAKEN AT THE BEGINNING POINT IN THE DECLINE OF T_A AND RISE OF T_H

1934 July	Air temp.		Tree temp.		T_A Up / T_H Down	T_A Down / T_H Up
	Up	Down	Down	Up		
14–15	74	34	35	14	$\frac{74}{35} = \frac{2.1}{1}$	$\frac{34}{14} = \frac{2.4}{1}$*
18–19	77	67	31	21	$\frac{77}{31} = \frac{2.5}{1}$	$\frac{67}{21} = \frac{3.2}{1}$†
19–20	72	26	25	12	$\frac{72}{25} = \frac{2.8}{1}$	$\frac{26}{12} = \frac{2.1}{1}$#
20–21	91	33	35	16	$\frac{91}{35} = \frac{2.6}{1}$	$\frac{33}{16} = \frac{2.0}{1}$¶
24–25	116	49	54	20	$\frac{116}{54} = \frac{2.1}{1}$	$\frac{49}{20} = \frac{2.4}{1}$§

* 1st T_A min. and T_H max. at intersection, 7:30 a. m.; 2nd T_A min. and T_H max., 2:30 a. m., 7/15.
† 1st T_A min. and T_H max., 8:15 a. m.; 2nd T_A min. and T_H max., 3:15 a. m., 7/19.
\# 1st T_A min. and T_H max., 6:30 a. m.; 2nd T_A min. and T_H max., 12:00 midnight.
¶ 1st T_A min. and T_H max., 7:00 a. m.; 2nd T_A min. and T_H max., 1:30 a. m., 7/21.
§ 1st T_A min. and T_H max., 6:00 a. m.; 2nd T_A min. and T_H max., 4:00 a. m., 7/25.

would be due to the declining air temperature of the preceding night. The only alternate explanation is that the low tree temperatures were due to a definite cooling concurrent with and related to the air-temperature rises of the daylight period. This latter is the hypothesis adopted in the earlier portion of this section. We will now consider the objections to the first of these alternate suggestions.

First, in the earlier part of the year the apparent lags due to rate of heat conduction through the tree tissues were, at the longest, about 1.5 to 2.5 hours, and sharper changes of air temperature caused an evident response even within an hour. Moreover, a study of the records shows that immediately after the intersections of T_A with T_H in the morning and afternoon the temperature usually continued its decline or rise respectively for 0.5 to 1 hour before the change in direction of the T_H

line can be detected. Hence the 1.5- to 2.5-hour lag includes the time when the influence of the preceding temperature was still operating. Actually, then, this apparent lag is longer than the true lag due to the heat conduction rate of the tissue. Second, the records at various seasons of the year show that when there was a deep and long depression of the air temperature below and before the morning intersection of T_A with T_H, especially with a slow rise in air temperature above the intersection, the apparent lag in rise of the tree temperature might be prolonged to 3 to 4 hours. With a shortening and decreasing of the cool period prior to the morning intersection of T_A and T_H the apparent lag period decreased. Therefore when there was no such depression below the tree temperatures, as during the latter part of July, 1934, there would be no apparent lag period and the cooling action would be immediately evident with rise of air temperature. Such was the condition during this hot spell of July, which is strong evidence also that the conditions recorded in the chart could not have been due to a 12-hour lag. Third, since the air temperatures during this entire period were, even at their lowest, higher than the highest point in the tree-center temperatures, a decline in the air temperature could not have lowered the tree-center temperature. Since the first explanation evidently cannot be accepted, the positive evidences in favor of the second alternative will be considered.

In passing from the early portion of the year toward the high-temperature period the apparent morning lag in T_H advanced from about 1.5 hours to about 3.5 hours (table v, column "d"). This lengthening of the apparent lag period cannot be assumed to be due to an actual change in the heat conductance of the tissues and hence a change in the true lag. Moreover, since the tissues involved are identical for the various years listed, no important difference in conductivity can be due to tissue differences. Therefore, this difference in apparent lag period can only be accounted for on the assumption of a cooling of the tissues which counteracted to a greater or less extent the heat from the rise in the air temperature. Furthermore, the following study of the records of several

TABLE V

INFLUENCE OF COOLING ACTION UPON "LAG"

Beginning of temperature rise*				Beginning of temperature fall					
a	b	c	d	e	f	g	h	i	j
(1930) July†	Air time	Center time	Diff. hours	Air time	Center time	Diff. hours	Air time	Cambium time	Diff. hours
24	10:00 a. m.	1:00 p. m.	3.0	8:30 p. m.	10:30 p. m.	2.0	8:30 p. m.	8:30 p. m.	0.00
25	6:30 a. m.	9:30 a. m.	3.0	10:00 p. m.	12:30 a. m.	2.5	10:00 p. m.	12:30 a. m.	2.5
26	6:45 a. m.	9:00 a. m.	2.25	11:30 p. m.	2:00 a. m.	2.5	11:30 p. m.	12:30 a. m.	1.0
27	7:00 a. m.	10:00 a. m.	3.0	10:45 p. m.	12:30 a. m.	1.75	10:45 p. m.	11:30 p. m.	0.75
28	7:30 a. m.	10:00 a. m.	2.5	11:15 p. m.	1:30 a. m.	2.25	11:15 p. m.	12:00 m.	0.75
(1932) June‡									
10	7:00 a. m.	9:30 a. m.	2.5	10:00 p. m.	12:30 a. m.	2.5	9:30 p. m.	10:00 p. m.	0.5
11	7:30 a. m.	10:30 a. m.	3.0	10:00 p. m.	12:00 p. m.	2.0	9:30 p. m.	10:00 p. m.	0.5
12	8:00 a. m.	11:30 a. m.	3.5	11:00 p. m.	1:00 a. m.	2.0	10:00 p. m.	11:00 p. m.	1.0
(1934) May#									
1	7:30 a. m.	9:00 a. m.	1.5	7:30 p. m.	9:30 p. m.	2.0	6:45 p. m.	7:30 p. m.	0.75
2	7:00 a. m.	8:30 a. m.	1.5	8:00 p. m.	9:15 p. m.	1.25	7:15 p. m.	7:30 p. m.	0.25
3	7:30 a. m.	10:00 a. m.	2.5	9:30 p. m.	11:30 p. m.	2.00	8:00 p. m.	9:30 p. m.	1.50
(1932) May									
13	7:30 a. m.	9:30 a. m.	2.0	11:00 p. m.	1:30 a. m.	2.5	9:45 p. m.	10:30 p. m.	0.75
14	7:00 a. m.	9:30 a. m.	2.5	11:30 p. m.	1:30 p. m.	3.0	10:15 p. m.	11:15 p. m.	1.0
28	8:15 a. m.	9:45 a. m.	1.5	7:00 p. m.	10:00 p. m.	3.0	6:15 p. m.	7:00 p. m.	0.75
29	6:00 a. m.	8:00 a. m.	2.0	8:30 p. m.	10:30 p. m.	2.0	7:00 p. m.	8:00 p. m.	1.0
30	6:30 a. m.	9:00 a. m.	2.5	10:00 p. m.	12:00 p. m.	2.0	8:30 p. m.	9:00 p. m.	0.5

(1934) April									
1	6:00 a. m.	8:30 a. m.	2.5	8:15 p. m.	9:30 p. m.	1.25	7:00 p. m.	8:00 p. m.	1.00
2	7:00 a. m.	8:30 a. m.	1.5	12:00 p. m.	1:30 a. m.	1.50	10:00 p. m.	10:30 p. m.	0.50
3	8:15 a. m.	10:15 a. m.	2.0	8:00 p. m.	9:30 p. m.	1.50	7:00 p. m.	7:30 p. m.	0.50
4	7:30 a. m.	8:30 a. m.	1.0	5:00 p. m.	6:00 p. m.	1.00	5:00 p. m.	5:15 p. m.	0.25
9	7:00 a. m.	8:00 a. m.	1.0	7:30 p. m.	9:30 p. m.	2.00	7:00 p. m.	7:15 p. m.	0.25
10	8:30 a. m.	9:00 a. m.	0.5	8:15 p. m.	9:30 p. m.	1.25	6:30 p. m.	7:30 p. m.	1.0
12	9:00 a. m.	10:30 a. m.	1.5	6:30 p. m.	8:30 p. m.	2.00	5:30 p. m.	6:30 p. m.	1.0
(1932) March									
18	7:45 a. m.	9:30 a. m.	1.75	9:45 p. m.	11:00 p. m.	1.25	7:15 p. m.	8:15 p. m.	1.00
19	8:00 a. m.	9:30 a. m.	1.5	6:15 p. m.	8:30 p. m.	2.25	5:45 p. m.	6:00 p. m.	0.25
20	10:30 a. m.	12:00 m.	1.5	7:30 p. m.	10:00 p. m.	2.50	6:30 p. m.	7:00 p. m.	0.50

* Following the principles indicated under Nos. 2 and 3 of the section on "Methods," the beginning of air-temperature rise and fall is taken at the intersection of T_A with T_H and T_C.

† During the latter part of July, 1930, a considerable cooling action was evident in increasing the "lag" periods, as shown in columns "d" and "g," and to some extent in column "j." On July 29 the tree-center temperature did not rise until after the air temperature began to decline in the p. m., by which time the cooling action was sufficient to neutralize completely the effect of the rise in air temperature.

‡ The same type of record was shown June 10–12, 1932. Before and after these dates definite cooling action was evidenced by the lack of rise in the tree-center temperature during the a. m. rise of the air temperature.

May 4, 5, and 6 show little rise until the p. m. decline in T_A and with T_C closer to T_H than before.

specific cases will give clear evidence of the validity of the concept of a positive cooling action in the tissues, and the difficulty in accounting for the curves on the basis of a "lag" of several to 12 hours.

In early June, 1934 (e.g., June 3, 4, 5, etc.), the maximum temperature of the cambium was reached approximately 2 hours before that of the center, while the air temperature was falling, sometimes even below the tree temperatures, as on June 5 at 12:00–5:30 a. m. The high air temperature preceding the high tree temperature was at about 1:30 p. m., the day before, with a secondary high at 4:30–5:30 p. m. (30° C.), or in other words 10 to 12 hours before. This rise of the tree temperature, both center and cambium, could not be ascribed to "lag" due to slow conduction of heat from the outside, because of the great length of time. Therefore it must be ascribed to an actual warming up of the inner tissues due to the slow removal of the cooling action.

The records show that on May 13 and 14, 1932, there was a period of 1.5 to 2 hours from the morning intersection of T_A with T_H to the beginning of the rise in T_H, while on May 15 there was no rise at all until the afternoon decline in T_A began. The 1.5- to 2-hour period is the usual interim, which represents the maximum true lag in the beginning of the reaction of the tree-center temperature to a change in air temperature. The lack of such a lag period on May 15 indicates that the cooling action within the tree was sufficient to counteract the incoming heat. In other words, due to the cooling action, the 43 "degree-hours" change of the atmosphere was unable to raise the temperature at the center of the tree. On May 14 a 12° rise in the air temperature caused a rise of only two degrees at the tree center while on May 15 a 15.5° rise failed to change the tree-center temperature.

During the night of June 3–4, 1932, the tree-temperature lines and that of the air were superimposed for about 13 hours, and about 5 a. m. the air temperature began a slow rise. At about 8 a. m. the tree-center temperature began to rise, and a total rise of 10.00° in the air temperature resulted in a 1.25°

rise in the tree center. During the next several days the tree-center temperature showed no rise except in association with the afternoon decreases in the air temperature. Here again on the first of these days the cooling action was not quite sufficient to neutralize the heat which penetrated from the atmosphere, while on the several following days it was sufficient. The records for July 13, 14, and 15, 1932, are typical of a large number of those for that month, which show that the cooling action was sufficient to prevent any heating of the tree center. During most of this period the cambium temperature was held at 1 to 2° above the center temperature, with little evidence of being influenced by the air temperature. This condition contrasts with that in March and April, as, for example, April 29, 1934, where the cambium temperature was influenced much more by that of the air and averaged 3° or more above that of the tree center. Even at this time, however, there was probably a considerable cooling action, since a few days later, by May 3 and 4, there was only a slight rise of temperature in the tree center. The record of March 19, 1932, illustrates the relationship of the three lines when little affected by the cooling action within the tree. Here there was an average difference between the T_H and T_C lines of about 4°, and the T_C line was almost in mid-position between the T_H and T_A lines.

A comparison of the spread of the three temperature lines during the latter part of June and the month of July, 1934, (table VI) shows that in general while the distance between the air-temperature and the tree-center-temperature lines (T_A max. minus T_H min.) increased greatly with the hotter weather, the distance between the air-temperature and the cambium-temperature lines (T_A max. minus T_C) averaged about the same throughout the whole period. Since, moreover, the distance between the two tree temperature lines (T_C minus T_H min.) increased greatly, the cooling action must have increased much more at the center than at the cambium. That the center cold zone was somewhat more effective in cooling the cambium at high temperatures than at lower ones is shown by the fact that there was a greater increase in the air temperature from

the early part of the period to the latter part than there was in the cambium temperature.

TABLE VI

T_H MIN., T_A MAX., AND T_C AVERAGE, JUNE AND JULY, 1934*

(1934) June	T_H min.	T_A max.	T_C average	Diff. T_A max. and T_H min.	Diff. T_A max. and T_C	Diff. T_C¶ and T_H min.
19**	19.5–21.5	31.75	20.00–24.00	11.25	9.75	1.5
20**	21.5–23.0	33.50	22.50–25.25	11.25	10.25	2.0
21	23.25	33.00	25.00	9.75	8.00	1.75
22	23.25	34.00	25.00	10.75	9.00	1.75
23	24.75–25.25	37.00	26.25	12.00	10.75	1.25
24	25.00	36.00	27.00	11.00	9.00	2.00
25	24.50	35.75	26.50	11.25	9.25	2.00
26	25.00	36.25	27.00	11.25	9.25	2.00
27	25.50–25.75	37.75	27.75	12.00	10.00	2.00+
28	25.75	37.75	27.75	12.00	10.00	2.00
29	26.00	38.00	28.00	12.00	10.00	2.00
30	irregular		26.25			
July						
1†‡	21.50	33.50	25.00	12.00	8.50	3.50
2	20.75	36.00	26.00–27.25	15.25	9.50	5.75
3#	19.00	37.00	26.75–27.50	18.00	10.00	8.00
4	18.00	36.00	27.00–27.75	18.00	8.50	9.25
5	18.00	36.50	28.00	18.50	8.50	10.00
6	19.50	29.00				
		irregular	27.00	9.50	2.00	7.50
7†	17.75	31.00	26.00	13.25	5.00	8.25
8	17.25	31.50	25.75–26.75	14.25	6.25	9.00
9†	20.50	32.00	26.00–27.00	11.50	5.50	5.75
10	18.00	34.25	25.00–28.00	16.25	7.75	8.50
11	20.00	37.00	27.50–31.00	17.00	7.75	9.25
12	19.75	39.50	27.50–31.00	19.75	10.25	9.50
13	18.75	39.50	29.25–31.00	20.75	9.25	11.50
14	18.00	36.75	27.50–29.25	18.75	8.75	10.25
15	18.00	38.75	28.50–30.50	20.75	9.25	11.00
16	19.50	37.00	29.50–30.00	17.50	7.25	10.25
17	17.75	32.25	28.25	14.50	4.00	10.50
18	16.75	38.75	27.75–30.75	22.00	10.00	12.50
19	17.50	39.25	29.25–30.75	21.75	9.75	12.50
20	16.50	42.00	30.50–31.75	25.50	11.00	14.50
21	17.00	40.00	30.25–31.50	23.00	9.25	13.50
22	17.50	38.75	30.25–31.00	21.25	8.25	13.25
23	15.50	41.50	29.25–32.00	26.00	11.00	15.00
24	15.25	42.00	31.25–32.25	26.75	10.25	16.50
25	16.00	42.00	31.25–32.25	26.00	10.25	15.75
26	17.00	32.75	29.50	15.75	3.25	12.50

* In degrees centigrade.
** Both T_H and T_C rise with T_A.
† Slight a. m. intersection of T_A with T_H.
‡ T_C farther from T_H.
# No a. m. intersection of T_A with T_H.
¶ Intermediate values sometimes used for T_C.

On July 16, 1934, at 7:00–7:30 p. m., a sharp drop in the atmospheric temperature not only resulted in a sharp rise in the tree-center temperature but also in about a 0.5° temporary rise in the cambium temperature. This was immediately followed by a decline in the latter as the air temperature dropped. The immediate inverse response in the tree to air-temperature change definitely indicates the instantaneous nature of the thermostatic action. Often, even in minor fluctuations, this is shown in the records of the high temperature period (table VII).

TABLE VII

EXAMPLES OF MINOR, INVERSE REACTIONS TO TEMPERATURE CHANGES

(1934) July	Hour	Air-temperature change	Tree-temperature changes	Notes
14	9:30–10:00 a. m. 5:30–6:00 p. m.	1.5° decline Slight rise	Cambium and center rise Slight center drop	
15	1:30 p. m.	1.0° rise	1.0° drop	
16	10:00–11:30 a. m.	3.5° rise	1.0° center drop 0.5° cambium drop	Further air-temperature and center change
17	4:00–6:00 a. m.	2.25° drop and then a. m. rise	About 0.5° rise and then a. m. drop	Several further minor fluctuations
18	10:30–11:30 a. m.	6.5° rise	3.0° center drop	Several further fluctuations and reverse responses
19		Several fluctuations	Several reverse responses in center	
24	11:00–11:30 a. m. 3:30–4:30 p. m.	Sharp increase in temp. rise Sharp drop and rise	Sharp drop 1.5° center Sharp rise and drop in center and slight effect on cambium	

On each of these days also the beginnings of the rapid morning rise of air temperature and of afternoon decline are associated with immediate reverse changes in the tree temperatures, so that in general the T_H line is usually a mirror image of the T_A line. These examples not only clearly indicate the almost

instantaneous nature of the thermostatic action, but also give positive evidence that the active cooling of the tissues is a response to the air-temperature rise.

After considering the various positive evidences just cited it can hardly be doubted but that thermostatic cooling is a major factor in determining the tree temperatures during the high-temperature periods of the year. Other phenomena associated with the summer periods will now be considered.

The morning sharp rise in the cambium temperature, during this period, which parallels that of the air temperature, may be due to either one of two factors or a combination of them. It may be assumed that in the morning a certain amount of direct insolation of the tree trunk might have taken place in spite of its being shaded by the heavy foliage. There are no direct observations upon this point. On the other hand, it may be assumed that the sharp rise in air temperature generally caused the corresponding rise in the cambium temperature. It appears from a tabulation that these sharp rises in the cambium temperature began essentially at the same time, about 7:30 each morning. Direct insolation could have been the cause, since the sun's rays would have been at the same angle each day over this short period of time.

On the other hand, there was a direct relationship between the intersection point and the beginning of the rise in T_c, usually a 15-minute interval only, which coincides with the lag in cambium-temperature at other times in the day and other seasons of the year when direct insolation would be impossible. There is then no conclusive evidence on this point, although the case next cited indicates direct insolation as a factor at this time of day.

The cambium temperature during the night of July 13–14, 1934, began a slow decline at about 11 p. m., which continued until about 4 a. m., when a 3° drop in 3.5 hours occurred, resulting from an almost synchronous sharp drop in the air from 27.75 to 22.00° C. Incidentally it may be noted that there was a "lag" of about 15 minutes between the beginning of the sharp drop in the temperature of the air and the beginning of the 3°

drop in the cambium region. From 7:30 a. m. until about 10:15 a. m., this region remained steadily at about 28.25° C. Since both the air and center had lower temperatures the cambium should have continued to drop due to continued radiation of heat to them. That it did not do so is indicative that a source of heat sufficient to balance the radiation from the cambium must have been present. Direct insolation is thus suggested.

It will be evident from the following discussion that thermostasy was not confined to the excessively hot dry period of late July in 1934. An intermediate condition is shown on the record for July 14, 1934, when the air temperature dropped below that of the tree center for approximately 3 hours during the early morning. Except for this early morning drop, the record is essentially like those which followed it. The T_H line began to drop from 25.00° C. about 1.75 hours after the T_A line first crossed the T_H line, at which time the temperature of the air fell below that of the tree center. For about 1.25 hours the tree-center temperature dropped in response to the lower air temperature. Then the T_A line re-crossed the T_H line due to the daily rise in air temperature. After that the T_H line continued its downward course, but now the decreasing center temperature was due mainly to the thermostatic action associated with the rising air temperature. That this decreasing tree temperature is due to one factor in part of the curve and to another factor in another part emphasizes both the necessity of a careful analysis of the records and one cause of misinterpretation of former records in which intermittent and partly correlated observations were made.

On July 2, 1934, about 5 a. m., the air temperature dropped somewhat below that of the tree center and under its influence the latter continued to decline. At 7 a. m. the air-temperature line re-crossed that of the center temperature, which continued to drop with a slight acceleration until 10 a. m. This decline may perhaps be considered as due to: (1) the "lag" in response to the former air-temperature decline, and (2) an acceleration of this drop due to thermostasy. That the latter is a real factor can be seen from the further changes of the two temperatures.

From 9 to 10:30 a. m. the air temperature was almost steady, though with a drop of 1° during the last 0.75 hour. At about 10:30 the center line leveled out, thus showing that the flow of heat in from the heated air and out through the cooling action had attained a temporary equilibrium. When at 11:30 the air temperature began to rise again the center temperature responded by a slow decline of 0.50°, beginning about 0.5 hour later. A decline of air temperature of 2° in 1.5 hours, beginning at 1 p. m., was registered an hour later in the center by the beginning of a rise of nearly 0.5°. The air-temperature rise, starting at 2:30 p. m., was reflected in the center an hour later by the beginning of a decline of 1.25°. The final decline in air temperature for the day began at about 5:15 p. m., and the final rise of the center temperature began about an hour later. This analysis of the fluctuations in the day's records shows that there was a "lag" of about one hour in the response of the tree center to air-temperature changes. It should be clearly understood that this type of "lag" is in no way similar to the "lag" which may be due to slow conduction of heat into or out of the tree. At a later stage in the water deficit in the tree (July 15–30) there was essentially no lag in this internal thermostatic action.

On July 26–28, 1930, the temperature reached a maximum each day of 39–41° C., following a long period of medium-high temperatures with maxima between 25 and 35° C. The tree temperatures during the earlier period had varied plus or minus 1 to 2° around 25° C. During the 3-day period under consideration this variation had shifted to plus or minus 1 to 2° around 30° C., with the center during the maximum periods about 2° lower than the cambium. Two additional phenomena are especially notable during this period. First, when the air temperature was at its maximum, the center temperature was approximately 10° below it, and its own maximum was 7 or more degrees below the air maximum. Second, on the third day, which was the hottest, the center and cambium regions were both cooler than on the preceding day as evidenced in table VIII.

TABLE VIII

(1930) July	Time	Max. air temperature	Tree-center temperature	Tree-cambium temperature	Degree-hours between 30° line and air-temperature line
26	3:00 p. m. 5:00 p. m. 9:45 p. m.	38.75° C.	29.75° C. 31.25° C.	31.50° C. 32.00° C.	82
27	3:00 p. m. 5:30 p. m. 11:00 p. m.	40° C.	30° C 31.25° C.	31.75° C. 32.00–° C.	95
28	3:30 p. m. 5:30 p. m. 11:00 p. m.	41° C.	29.75° C. 31.25° C.	31.50° C. 31.75° C.	103

In addition, although the maximum air temperature on July 28 was 2.25° higher and there were 21 more "degree-hours" of change than on July 26, the tree temperatures were the same on both days. This indicates clearly that during the summer period of 1930 the same cooling action which was so sharply evident during the excessively hot dry spell of 1934 was effective in keeping the tree temperatures well below those of the air. It should be noted again that since during periods of low to moderate air temperatures the tree-temperature graphs often are almost superimposed upon that of the air, at higher temperatures a great resistance is evidently offered by the tree tissues to increase of temperature. This cannot be due to slow conduction of heat through the tissues, since in this set of observations the same set of tissues was involved throughout, and relatively rapid response, together with a temperature essentially equal to that of the air, was very frequent. The "lag" which has been heretofore ascribed to slow heat conduction and heat radiation is therefore due not only to these factors in part, but also to this thermostatic cooling of the tissues.

During large portions of July and August, 1932, both tree temperatures held steadily between 25 and 30° C., with only slight movement up and down in response to the daily and nightly swings of 10° in the air temperature. This resistance by the tree to change of temperature during considerable

changes in air temperature may now definitely be ascribed to the thermostatic action and not mainly to "lag" induced by slow heat conduction.

On July 29, 1930, the cooling effect on the tree temperatures is shown by the fact that, following the intersection of T_A with T_H and T_C during the morning rise of T_A, the line representing T_H dropped as T_A increased and the rise in T_C was postponed for 3 hours, until 12:30 p. m. During the preceding days it had varied only from 0.25 to 0.75 hour later than the intersection of T_A and T_C. For the entire period of July 23–28, 1930, an increased cooling action in the tree is evidenced by the increase of the difference between the tree-temperature maxima and the air-temperature maximum as seen in table IX.

TABLE IX

(1930) July	T_A max.	T_H max.	Diff. T_A and T_H	T_C max.	Diff. T_A and T_C
23	31.50	26.25	5.25°	26.75	4.75°
24	30.00	25.75	4.25°	26.00	4.00°
25	36.00	27.75	8.25°	28.75	7.25°
26	38.75	31.25	7.50°	31.75	7.00°
27	40.00	31.00	9.00°	31.75	8.25°
28	41.00–	31.25–	9.75°	31.75	9.25°
29	33.75	28.25	5.50°	29.00	4.75°

For all of these periods, during which a definite thermostatic cooling can be demonstrated, the number of "degree-hours" of air-temperature rise required to cause one "degree-hour" rise in the tree center is indicated in table x. In general, it can be seen that the ratio rises from about 3:1, when the cooling action due to transpiration would be none or slight, to much higher ratios as the season advances until in certain cases little or no rise takes place in the tree in response to the rise in air temperature. The next step is the positive reduction of tree temperature during the air-temperature rises. The variability in the ratios may be accounted for by the action of other factors than air temperature as discussed in a later section.

It is clear from the records just cited that the thermostatic cooling of the tree tissues is a phenomenon present at least dur-

ing the warm portions of the year and not simply under the extreme temperature conditions such as existed in the latter portion of July, 1934.

TABLE X

DEGREE-HOUR RATIOS AT VARIOUS SEASONS OF THE YEAR*

(1934) March	ABD	EFG	Ratio ABD/EFG	T_A max.	
15	83	29	2.8:1	15.50° C.	2 hrs.
16	42	16	2.6:1	17.00° C.	2 hrs.
17	37	10	3.7:1	22.00° C.	2 hrs.
29	87	30	2.9:1	19.00° C.	2 hrs.
30	55	14	3.9:1	22.25° C.	3 hrs.
April					
1	72	24	3:1	18.00° C.	5 hrs.
2	93	30	3.1:1	24.50° C.	3 hrs.
14	94	34	2.4:1	23.50° C.	2 hrs.
16	58	16	3.6:1	20.00° C.	2 hrs.
17	52	18	2.9:1	20.00° C.	3 hrs.
18	69	25	2.7:1	26.50° C.	2.5 hrs
23	76	19	4.0:1	27.00° C.	1.75 hrs.
25	39	9	4.3:1	20.00° C.	1 hr.
27	21	7	3:1	15.00° C.	2 hrs.
28	51	15	3.4:1	18.50° C.	2 hrs.
29	63	18	3.5:1	24.00° C.	1.5 hrs.
May					
3	44	8	5.1:1	27.50° C.	2 hrs.
6†	66	9	7.3:1	29.00° C.	1 hr.
7†					
8†	40	1	40.0:1	29.50° C.	2 hrs.
9†	71	3	23.0:1	33.25° C.	2.5 hrs.
12	53	10	5.3:1	28.25° C.	2 hrs.
16	66	16	4.1:1	24.00° C.	3 hrs.
17	69	15	4.6:1	28.50° C.	1.5 hrs.
18†	69	9	7.6:1	29.50° C.	1 hr.
19–22†					
23	50	10	5:1	26.75° C.	2 hrs.
25	29	10	2.9:1	21.50° C.	1.5 hrs.
26	58	15	3.8:1	23.75° C.	1.5 hrs.
27	75	15	5.0:1	26.25° C.	4 hrs.
28	129	23	5.6:1	29.25° C.	2.5 hrs.
29	100	13	7.7:1	33.00° C.	2 hrs.
30†					
31†					
June					
3†					

* In calculating these areas the boundary of the tree temperature area was raised 1.5 hours to make up for the 1.5-hour "lag" approximately, which occurs in the initiation of the rise of the tree temperature after the intersection of the T_A with the T_B line during the morning rise of T. 1.5 hours past the *last point* of air maximum taken as line FG. (See fig. 4.)

† Shows inverse relation of T_B to T_A in p. m.

TABLE X—(Continued)

(1932) June	ABD	EFG	Ratio ABD/EFG	T_A max.
12	45	5	9:1	
13	28	4	7:1	
14	16	1	16:1	
15	33	4	8.2:1	
16	59	6	10:1	
17	63	7	9:1	
29	63	10	6.3:1	
July				
14	55	2	27.5:1	
15	56	3	18.7:1	
(1930) July				
24	23	5	4.6:1	
26	74	15	5:1	
27	69	7	9.8:1	
28	66	5	13.2:1	
29	24	1	24:1	

MEDIUM TEMPERATURES

Many of the principles previously discussed are applicable to the medium range of temperatures, and some "case studies" in this range were necessarily considered in former sections of this paper. The demonstration of thermostasy in this temperature range is important as indicating that it is a general phenomenon which is one of the significant factors determining the tree temperatures.

Evident cooling of both center and cambium tissues, associated with air-temperature increases, shows clearly on the record of early July, 1934, when both failed to follow the upward trend of the air temperature and when the center temperature had even a slight downward trend. The thermostatic action is visually demonstrated in an especially striking manner on July 5, when at 2 p. m. a sharp *drop* in the air temperature of almost 5.0° was reflected immediately in a sharp *rise* of the center temperature of slightly over 0.5°. This contrasts sharply with the normal condition at periods of the year when foliage and therefore active transpiration are absent.

EARLY EVIDENCES OF THERMOSTASY IN 1934

Between 6:15 and 6:30 p. m., June 17, 1934, there was a sharp drop in the air temperature from 30.25 to 19.50° C. At the same time the center and the cambium temperatures took an upward trend, the latter somewhat more marked. This was followed by a general downward movement, the center beginning 1.5 hours after T_A crossed T_H, associated with the continued drop in the air temperature. Two things are shown at this date: (1) the direct and immediate dependence of a rise in the tree temperatures on a drop in the air temperature, and hence the presence of a prior cooling action; and (2) an interval of only 1.5 hours between the intersection of the air line with the tree-center line and the beginning of the decline of the tree-center temperature.

In the latter part of June, 1934, as, for example, June 26, a balance was evident between the transfer of heat inward and the heat removed by the cooling action. From 7 a. m. to 5 p. m. a temperature of 25° C. was steadily maintained in the center of the tree while the air temperature increased from 25° to 36.25° C. in six hours and remained at about that point for 4 hours. At 5 p. m. the air temperature began to drop and simultaneously the tree-center temperature began to rise. This same reaction is traceable through the records of many days from early in May onward through June and July. At this period of the year the daily downward tendency of tree-center temperature usually began coincidentally with the rise in the air temperature. However, when the air temperature dropped for a few hours below that of the tree center, as, for example, from 1:00 to 7:00 a. m. on June 22, there was at times a slow drop in the tree temperatures. This downward movement, due to air cooling, frequently merged into the cooling associated with the rise in the air temperature, but the latter caused an acceleration in the rate of cooling. Thus, on June 22 the rate of cooling just prior to the intersection of the air line with the center line was 0.5° in 2 hours, while immediately following this intersection it was 0.5° in less than an hour. During the latter part of June the period of steady low temperature in the tree center

became longer, indicating an increasing amount of cooling action with the advance of the season.

On June 1, 3, and 4, 1934, a sharp drop and subsequent rise in air temperature occurred each afternoon, and at the same time a small bend upward and downward in the tree-temperature lines appeared. These inverse responses to air temperature changes are identical in type with those which occurred during the high-temperature period of the latter part of July, and indicate clearly the concurrent nature of the air-temperature changes and the inverse tree-temperature changes.

For several hours on June 26 and 27 the air temperature was maintained at 36 and 37° C., which was as high as on some of the days during the later period of July. Yet the cooling of the center of the tree was much less marked, which shows that high temperature alone was not sufficient to occasion the excessive thermostatic action of July, 1934. At air temperatures which averaged below 35° C., as in a long period prior to June 26, the two tree temperatures were very close, usually not more than 2° apart, thus giving evidence of thermostatic cooling of the cambium. On several days during May (6–9, 18–22, 30 and 31), 1934, the tree-temperature line showed definitely a greater rate of increase at about the point on the air-temperature line where the afternoon decrease began. For some of these days also it is impossible to calculate a ratio between the T_A rise and T_H rise, since no evident increase in tree temperature took place until this afternoon inflection of the two lines showed on the record. This lack of rise in the tree temperature in the early part of the day, at the time that the air temperature was increasing, can only be explained by a cooling action within the tree associated with increasing air temperature, and the rise at the time of the air-temperature decrease must be due to a decreasing cooling action associated with decreasing air temperatures. This may be demonstrated also in the following manner. The period of temperature rise in the tree center may be divided into two portions, the first, up to the time of the beginning of the afternoon decline in the air temperature, and the second after that time. During the first portion the increasing

air temperature, if there were no concurrent cooling action, should have caused a more rapid rise in the tree temperature than during the second, when the air temperature was actually falling. If the rate of rise in the tree temperature was greater in the second than in the first portion it would indicate an excess of cooling action during the first portion of the curve. The following data for several of the days in May, 1934, thus clearly indicate thermostatic cooling at this period.

May 3—T_H minimum, 19.25° C. at 9:30 a.m.
T_H at 4:30 p.m., 21.25° C. or 2.0° rise in 7 hours.
T_H at 9:00 p.m., 22.00° C. or 0.75° rise in 4.5 hours.
Rate during 1st portion of rise, .28° C. per hour.
Rate during 2nd portion of rise, .16° C. per hour.

Here it is evident there was no excess cooling action, since the rate in the latter portion of the curve was much less than during the first portion. The values for other days in May, calculated in similar fashion, are listed below:

May 4—Rate 1st portion of curve, 0.05° per hour.
Rate 2nd portion of curve, 0.25° per hour.
May 6—Rate 1st portion of curve, 0.11° per hour.
Rate 2nd portion of curve, 0.25° per hour.
May 8—Rate 1st portion of curve, no rise discernible.
Rate 2nd portion of curve, 0.17° per hour.
May 9—Rate 1st portion of curve, 0.11° per hour.
Rate 2nd portion of curve, 0.25° per hour.
May 29—Rate 1st portion of curve, 0.33° per hour.
Rate 2nd portion of curve, 0.41° per hour.

Considerable rates of increase are therefore evident on May 4, 6, 8, 9, and 29, during the second portions of the curves, thus indicating cooling action during the first portion.

The record for May 31, 1934, may be studied as a typical example during the portion of the year when medium temperatures dominated and the thermostatic cooling definitely affected the tree temperatures (table XI derived from the graph-record). The beginning of the rise in air temperature and the

beginning of the daily increase in the rate of decline in the tree temperatures were coincident, at about 5:30 a. m. From about 8:30 a. m. to 5:00 p. m. the tree center remained steadily at 22.75° C., and the cambium slowly rose from 24.50 to 24.75° C. At 5:00 p. m. the air temperature began its usual decline and simultaneously the tree temperatures began to rise, for one hour very slowly and then more rapidly.

TABLE XI

DATA FOR RECORD OF MAY 31, 1934

Item	Time	Temp. ° C.	Rate per hour
1. 1st T_A min.	5:30 a. m.	22.00	
2. 1st intersection of T_A and T_H	6:30 a. m.	24.00	
3. T_H min. (beginning)	12:15 p. m.	22.75	
4. T_A max. (beginning)	12:15 p. m.	35.00	
5. T_A max. (end)	5:00 p. m.	35.50	
6. Beginning 2nd phase of p. m. rise in T_H	6:30 p. m.	23.00	
7. 2nd intersection T_A and T_H	1:30 a.m. 6/1	25.50	
8. T_C min.	8 a. m.–5 p. m.	24.25–24.75	
9. 2nd intersection T_C and T_A	11:15 p. m.	26.75	
10. 2nd T_C max.	12:00 p. m.	26.75	
11. Beginning 1st phase p. m. rise in T_H	5:00 p. m.	22.75	
12. Beginning 1st phase p. m. rise in T_C	5:00 p. m.	24.75	
13. Beginning 2nd phase p. m. rise in T_C	6:00 p. m.	25.00	
14. Beginning 2nd phase p. m. decline in T_H	6:30 p. m.	32.50	
15. a. m. rise in T_A 4 minus 2	5.75 hrs.	11.00	1.91
16. Length of T_A max. 4 to 5	4.75 hrs.		
17. a. m. decline in T_H 2 minus 3	5.75 hrs.	1.25	0.21
18. p. m. decline in T_A 5 minus 11	8.50 hrs.	10.00	1.17
19. Total rise in T_H 7 minus 3	13.25 hrs.	2.75	0.20
20. 1st phase p. m. rise in T_H 11 minus 6	1.5 hrs.	0.25	0.166
21. 2nd phase p. m. rise in T_H 7 minus 6	7.0 hrs.	2.50	0.357
22. 1st period p. m. decline in T_A 5 minus 14	1.5 hrs.	3.00	2.000
23. 2nd period p. m. decline in T_A 14 minus 7	7.0 hrs.	7.00	1.000
24. 1st phase p. m. rise in T_C 13 minus 12	1.0 hrs.	0.25	0.250
25. 2nd phase p. m. rise in T_C 9 minus 13	5.25 hrs.	1.75	0.333

An inspection of the graph-record shows a small but definite bending downward of the tree-temperature lines at 5:30 a. m. coincidental with the beginning of the rise in the air temperature. This demonstrates an increase in thermostatic cooling when the air temperature was relatively low (i.e. 22.00° C.)

and below the tree temperatures, and shows that the cooling action was not necessarily associated with high temperatures. From the data in table XI it is evident that the rise in temperature of the tree, associated with the decline in the air temperature, occurred in two stages. During the first, while the air temperature was dropping at the rate of 2.0° an hour, the center and cambium rose at the rates of 0.166° and 0.25° an hour respectively. During the second phase, when the air-temperature rate of decline was 1.0° an hour, the center and cambium temperature rose 0.357° and 0.333° an hour respectively. Since it cannot be assumed that the rate of heat conduction increased, the data cited above demonstrate that the thermostatic cooling was more effective at higher air temperatures.

On June 17, 1934, from 6:00 a. m. to 3:30 p. m., there was a slow downward movement of the tree-center temperature from 26.00 to 25.00° C., almost coincidental with an increase in air temperature from 24.50° C. at 5:30 a. m. to 31.75° C. at 10:30 a. m., followed by sharp depressions and rises until about 6:15 p. m. At this time a sharp drop from 30.25 to 21.00° C. resulted in an immediate small swerve upward in the center temperature of about 0.5° and in the cambium of about 0.75° C. At about 3:00 p. m. both tree temperatures showed a small but distinct swerve downward in response to an increase in the air temperature from 25.00 to 31.25° C. About 0.5 hour after the intersection of T_A with T_C and 1.0 hour after the intersection of T_A with T_H in the afternoon the T_C and T_H lines began a slow decline in response to the lower air temperature. This was due to heat conduction outward from the tissues.

The record for June 17 emphasizes a number of important points. (1) At this date, well before the hot dry period of late July, the thermostatic action can be seen, not only from the calculations given in table XII but also from the curve where sharp changes in the air temperature occurred. (2) The compound character of the tree temperature due in part to heat gradients across the tissues and in part to the thermostatic cooling action is indicated. (3) That the temperature of the cambium, as well as that of the center, is in part due to a local

cooling of the tissues is demonstrated by the almost immediate reduction of the cambium temperature concurrent with the rapid increase in the air temperature and vice versa. (4) The phenomenon heretofore called "lag" is not simply due to slow conduction of heat into or out of and across the tissues as has been explained by other investigators. This can be demonstrated by a comparison of this record with the records for previous days, as indicated in table XII. On June 14, 15, and 16, for example, there was for each day an interval of from 10 to 12 hours between the middle of the maximum-temperature period of the air and the middle of the maximum-temperature period of the tree center. This formerly has been designated as a "lag" of 10 to 12 hours and ascribed to slow conduction of heat. On June 17, between 5:00 and 7:30 p. m., the sharp drop in air temperature, with mid-point at about 6:30, had its maximum effect upon the cambium and the center of the tree at 7:00 and 8:00 p. m. respectively, or 0.5 hour and 1.5 hours afterwards. Then the cooling action due to the lower air temperature began to reduce the tree temperatures. These intervals of 0.5 and 1.5 hours constitute a partial measure of the true "lag" in the usually accepted sense of that word. A heat gradient from the inner to the outer tissues sufficient to cause the beginning of a detectable decline in the center temperature was attained in about 1.5 hours. However, if an internal thermostatic cooling was taking place, then a decrease in the rate of this cooling due to decline in the air temperature would tend to neutralize for a while the loss of heat to the outside and thus extend the time before the beginning of the decline in the tree temperature. Hence the 0.5 hour and 1.5 hours represent more than the maximum which, under these circumstances, we should assign as the true "lag" period due to slow heat conduction. It is evident, in any case, that since there was little or no rise in T_H while T_A was at its maximum, the 10–12-hour difference between the maximum of the air and that of the tree center on June 14, 15, and 16 could not be due primarily to a slow conduction of heat inward across the tissues, but to a reduction in the cooling action.

TABLE XII

"LAG" BETWEEN T_A MAX. AND T_H MAX., JUNE, 1934

(1934) June	T_A max.*	T_H max.*	Diff. degrees	T_A max. time day	T_H max. time night	Diff. time
11	29.50†	23.75‡	5.75	1:30–5:30	1–3	10.5 hrs.
12	27.25‡	22.50‡	4.75	4:00–5:30	10:30–1:00	5 hrs.
13	29.75†	23.00‡	6.75	1:00–5:00	11–2	9 hrs.
14	28.75†	24.00‡	4.75	1:30–6:00	12:30–2:30	10 hrs.
15	31.75†	25.00‡	6.75	1:00–4:00	1:30–3:30	12 hrs.
16	33.25†	26.25‡	7.00	1:30–5:00	1:30–5:00	12 hrs.

* T_A max. and T_H max. taken as: † central line through a several-hour period of less than 0.50° variation, or ‡ the maximum held for more than 1 hour.

From the cases cited it is evident that at least during the period from early May, 1934, onward there was a thermostatic cooling which often was sufficient to more than overcome the effect of the heat from without. The cases cited will show that this phenomenon was associated not only with the year 1934, when there were exceptional conditions of heat and dryness, but also with other years under moderate temperature conditions.

In 1932 the thermostatic action is traceable back through July and June (at least to June 4) by the actual drop in the center temperature with the morning rise in the air temperature, and by the very slow concurrent rise in the cambium temperature. The latter also showed even on June 4 an accelerated upward movement when the air temperature began to drop.

During periods of moderate fluctuation of the air temperature, e.g., between 15° and 25° or 30° C., as during much of the month of May, 1934, the cambium and center temperatures usually kept within 1 to 2 degrees of each other, with the cambium usually a little higher. The rise and decline of the tree temperatures usually began within less than 2 hours after the intersections of the air-temperature line with the tree-temperature lines, the cambium temperature responding most rapidly. It has already been pointed out that when the tree temperatures were within 2 degrees of each other and the air temperature several degrees above that of the cambium a certain amount of thermostatic cooling was indicated. Usually

this type of record merged a few days later into that in which thermostasy was indicated by a long "lag" period between the morning intersection of T_A with T_H and the beginning in the rise of the tree-center temperature. The various stages in increasing thermostasy during the early part of the season can be seen by comparing successively the records of April 20, 24, 30, May 3, 4, and 5, 1932. On April 20 there was no evidence of cooling action, since (1) the T_H line began its rise 1.5 hours after the morning intersection of T_A with T_H; (2) the T_C line followed closely the rise in T_A and at least 4.0° above the T_H line; and (3) there was no inverse reaction of the T_C and T_H lines at the beginning of the T_A decline in the afternoon. On April 24 (1) the somewhat longer interval, about 2.25 hours, between the intersection of T_A with T_H and the beginning of the rise in T_H, and (2) the somewhat closer approach of the T_C to the T_H line, suggest a slight thermostatic action. A somewhat more pronounced, similar condition on April 30 and May 3 is further indication of increasing cooling action. On May 4 (1) the 3-hour morning postponement in the rise of T_H, (2) the slow rise of T_H and T_C, with a several-hour (ca. 6 hours) flattening of the T_C curve, during the rise in T_A, (3) the close paralleling of T_C with T_H, (4) the distinct rise in T_C concurrent with the decline in T_A, and (5) the inflexing of the T_H line as well, during the decline in T_A, all give clear evidence of thermostatic cooling at this time. All of these features are further strengthened in the record of May 5.

In this series of records thermostasy occurred at moderate air temperatures, with maxima around 30.0° C. for only short periods of the day. An inspection of the graph-records, however, will show that in general there was, through this period, an increasing amount of heat each day, as indicated by the greater area in the chart covered by the T_A line in the later days.

The normal direct reaction of the tree temperatures to changes in the air temperature, as shown in the cases cited below, contrasts in certain definite ways with the indirect thermostatic reaction just illustrated.

The records for March 18 and 19, 1932, are typical of the relationship of the three temperature lines at a time when the tree temperatures were not complicated by transpiration in the tree or by the zero-line adjustments. The cambium temperature was about 4 degrees higher than that of the tree center and was nearly halfway between that of the air and of the tree center. This may be used as one criterion for judging when cooling action became somewhat effective in retarding the direct influence of the atmospheric temperature upon the tree temperatures.

The fluctuations of 12.0 to 15.0° between the night and day air temperatures resulted in almost parallel advances and declines in the tree temperatures, with the latter below the air temperatures from about 8 a. m. to about 6 to 7 p. m., and above them during the night. The beginning of rise in the center temperature on March 19 was about 1.5 hours after the morning intersection of T_A with T_H. The center temperature attained its maximum 1.5 hours after the afternoon intersection of T_A with T_H.

On March 17, 1934, before foliage had developed, there was a sharp drop in the T_A line from 21.5 to 11.5° C. in about 0.75 hour. The T_H line continued its upward movement 0.5° above the intersection of T_A with T_H for about 0.5 hour, and the T_C line continued less than 0.25° above the intersection of T_A with T_C for about 0.5 hour. Both T_H and T_C, after retaining their maxima for about 1.0 and 0.5 hour respectively, began a steady fall for about 20 hours, gradually approaching the T_A line. This demonstrates the typical reaction of the tree temperatures to a very rapid change in air temperature when not complicated by the presence of transpiring foliage or other disturbing factors such as occur when the tree temperatures cross the zero line. The true heat diffusion "lag" was about 0.5 hour for the cambium and 1 hour for the tree center. The maximum T_A, which held for about 2 hours just before the sudden drop, was 22.0° C. The number of "degree-hours" of atmospheric change was about 37, producing about a 10 degree-hour change in the tree center or a ratio of about 3.7 :1. This appears to be

TABLE XIII

INFLUENCE OF RISE IN AIR TEMPERATURE ON TREE TEMPERATURE WHEN NOT DISTURBED BY FREEZING OR THERMOSTASY

(1932) Jan.	T_A min.*	T_A max.	Diff. degrees	T_A min. hour	T_A max. hour	Diff. hours	T_H min.	T_H max.	Diff. degrees	T_H min. hour	T_H max. hour	Diff. hours	$\frac{T_A \text{ rise}}{T_H \text{ rise}}$
27	0.00	9.00	9.00	7:30 a. m.	2:30–3:30 p. m.	7	0.00	5.50	5.5	10:15 a. m.	8:30 p. m.	10.25	$\frac{9.0}{5.5}$
28	6.50	16.00	9.50	7:00 a. m.	2:30–3:30 p. m.	7.5	5.50	11.50	6.0	9:30 a. m.	7:30–9:00 p. m.	10	$\frac{9.5}{6.0}$
Cold Spell													
Feb. 7	2.25	13.00	10.75	9:00 a. m.	5:00–6:00 p. m.	8.5	2.00	7.50	5.5	1:00 p. m.	12:00–3:00 a. m.	11	$\frac{10.75}{5.5}$
8	Cold Spell												
9	2.00	19.00	17.0	6:45 a. m.	3:00–4:30 p. m.	8	1.50	11.50	10	10:30 a. m.	11:30 p. m.–12:30 a. m.	12.5	$\frac{17.0}{10.0}$
10†	19.75	28.50	8.75	7:45 a. m.	12:30–1:30 p. m.	5	15.00	22.50	7.5	7:45 a. m.	6:00–7:30 p. m.	10.5	$\frac{8.75}{7.50}$
Cold Spell													
13	5.75	13.00	7.25	8:30 a. m.	2:30–4:00 p. m.	8	5.50	9.00	3.5	10:30 a. m.	7– 8 p. m.	9	$\frac{7.25‡}{3.5}$
Cold Spell below 10° C.#													

22	1.25	8.25	7.00	9:30 a. m.	3:00–5:00 p. m.	6.5	1.25	6.00	4.75	10:30 a. m.	7:30–10:00 p. m.	9	7.00/4.75
23	1.00	6.00	5.00	11:15 a. m.	3:30–4:30 p. m.	4.5	1.00	3.00	2.00	2:00 p. m.	9:00–12:00 p. m.	7	5.00§/2.00
24	1.50¶	17.50	16.00	8:30 a. m.	2:30–5:00 p. m.	7	1.50	11.25	9.75	10:30 a. m.	9–11 p. m.	11	16.00/9.75
25	7.50	22.25	14.75	8:00 a. m.	3:30–6:00 p. m.	7.5	7.25	16.50	9.25	10:30 a. m.	10–11 p. m.	12	14.75/9.25
26	12.25	21.25	9.00	11:30 a. m.	4:45–5:45 p. m.	5.5	12.25	16.75	4.50	11:00 a. m.	8:30–10:00 p. m.	9.5	9.00/4.50
27	12.50	18.25	5.75	10:45 a. m.	2:45–5:00 p. m.	4	12.25	15.25	3.00	11:30 a. m.	8.:00–9:30 p. m.	8.5	5.75/3.00
28	10.50	22.00	11.50	9:30 a. m.	4:30–5:30 p. m.	7	10.50	16.50	6.00	11:30 a. m.	9:30–11:30 p. m.	10	11.50/6.00
29	12.50	18.50	6.00	11:30 a. m.	2:30–5:00 p. m.	3	12.00	15.25	3.25	1:00 p. m.	5–10 p. m.	5	6.00/3.25

* T_H min. and T_A min. hour taken at time of actual beginning of new daily rise of T_A or T_H, and at intersection of T_A and T_H, if any, and above 0° C.

T_A max. hour taken at time of first attainment of T_A max.

T_A max. and T_H max. taken as average of maxima covering more than one hour and at least 0.5° change, especially in T_H.

† A continuous rise day and night from 7 a. m., Feb. 9, to 12:30 p. m., Feb. 10, required estimates of T_A min. and T_H min. and hours on Feb. 10. Total ratio for this period T_A/T_H = 26.50/21.00.

‡ A rapid and severe drop in air temperature carried the air-temperature line across the tree-temperature line before the T_H max. was attained and hence reduced the T_H max. The T_H line began to drop 2 hours after this crossing and 4 hours after the T_A line began its drop.

On Feb. 18 a rise in air temperature from 0 to 5.5° C. caused a 3.0° rise in the tree, a ratio of T_A/T_H = 5.5/3.0.

§ Very short T_A max. which was well below 10° C.

¶ 1.5° C. was the point at which the air-temperature line crossed the tree-temperature line in its daily rise. Below this point the rise in air temperature could not cause a rise in tree temperature.

the usual approximate, maximum ratio when the disturbing factors noted above are absent.

Various other early-season records showing thermostasy have been previously cited, so that there is ample evidence of the presence of this phenomenon at various seasons and in different years.

Direct insolation of the tree accounted for a rise in the cambium during certain parts of the season. For example, on March 14, 1934, at about 9 a. m. the cambium temperature began to rise from 6 to 8° C., while the center temperature remained steadily at 5.5° C. and the air temperature remained below that of the cambium. A similar situation existed on the morning of March 18, when the cambium rose from 1.0 to 2.25° C., while the air temperature was from 1 to 2° below zero. On April 12, 13, 19, 20, 21, 24, and 25, direct insolation caused a rise of about 3.0° in the cambium temperature under circumstances similar to those of March 14 and 18, and with no evident corresponding rise in the center temperature. Several other examples are to be found in the records, as on February 26 and 27, 1932, and on January 31 and February 1, 1931, when the cambium remained approximately 2.5° higher than the atmosphere for from 3 to 4 hours.

The direct effect of air temperature upon the tree temperature is well shown in table XIII under the column T_A rise/T_H rise. It is evident from these data that since the ratio never reached 3:1, less than 3° of air-temperature rise was needed to cause a rise of 1° in the tree center. This period of the year was of course free from the complication of thermostatic cooling or other effects due to the presence of foliage and its transpiration. It will be noted that this rule held at all temperatures above 0° C. and when the minimum air temperature was at or above that of the tree. When the air temperature was below that of the tree it of course could not raise the tree temperature, and in preparing the table all air temperatures below the minimum tree temperatures were ignored. Any heat derived from direct insolation of the tree trunk at the thermometer level would tend to increase the factor "T_H rise" and thus lower the

ratio. That this possible disturbing factor probably did not seriously alter the ratio is indicated by a comparison of the ratios in table XIII with those between the temperature drop of the air and of the tree at night during this same period, as seen in table XIV. The average ratio during the day was about 1.71:1 and during the night about 1.64:1.

Discussion and Conclusions

LAG

In former publications the word "lag" has been used to cover any departure in time between an air temperature and a supposed correlative tree temperature. Most frequently it has been used to cover the period between an air-temperature maximum or minimum and the following tree-temperature maximum or minimum respectively, on the assumptions, first, that the transfer of heat into or out of a tree requires time, and second, that the tree-temperature maximum or minimum is directly and only due to the preceding air-temperature maximum or minimum more or less modified by factors of relatively slight importance. The first of these assumptions is of course correct, but many authors have also tacitly assumed that the time consumed in the transfer of heat would vary from time to time in the same tree as well as in different trees. The second assumption, as has been demonstrated in this investigation, will have to be fundamentally and seriously modified, although it is clear that the air-temperature changes under certain conditions are reflected directly, in modified form, in the changes in the tree temperatures.

An examination of the records as already presented demonstrates that the rate of conduction of heat across the tissues is for an individual at a given place a constant, which under the given conditions may be stated as follows: A readily detectable change of temperature at the cambium layer occurred in less than 0.25 hour and in the tree center in less than 1.5 hours. For purposes of this paper these periods of time have been called the "true lag" periods. Theoretically a change of temperature

TABLE XIV
INFLUENCE OF REDUCTION OF AIR TEMPERATURE ON TREE TEMPERATURE

(1932) Feb.	T_A max.	T_A min.	T_A loss*	T_H max.	T_H min.	T_H loss	Ratio $\frac{T_A \text{ loss}}{T_H \text{ loss}}$
7–8	7.50	0.00	7.5	7.5	4.5	3.00	$\frac{7.5}{3.0}$
12–13	17.75	2.00	15.75	17.75	5.5	12.25	$\frac{15.75}{12.25}$
13–14	13.00	5.25	7.75	9.00	1.0	8.00	$\frac{7.75}{8.00}$
19–20	5.00	–3.00	8.00	5.00	–1.00	6.00	$\frac{8.00}{6.00}$
22–23	5.00	–1.5	6.5	5.00	1.00	4.00	$\frac{6.50}{4.00}$
24–25	11.00	4.00	7.0	11.00	7.25	3.75	$\frac{7.00}{3.75}$
25–26	16.00	8.5	7.50	16.00	12.25	3.75	$\frac{7.50}{3.75}$
26–27	16.25	9.00	7.25	16.75	12.25	4.50	$\frac{7.25}{4.50}$
27–28	15.50	6.00	9.50	15.50	10.50	5.00	$\frac{9.50}{5.00}$
28–29	16.50	7.00	9.50	16.50	12.00	4.50	$\frac{9.50}{4.50}$
29–3/1	15.25	9.00	6.25	15.25	10.50	4.75	$\frac{6.25}{4.75}$

* The decrease in air temperature (T_A loss) was taken between the point of intersection of the air-temperature line with the tree-temperature line (the T_A max.), and the point of actual minimum air temperature (T_A min.).

at the surface of the tree would be propagated through the tissue at a very high rate, of the order of the propagation of any other true wave in elastic matter, and in general determined by the thermal conductivity of the tissue. Since the detection of the change would depend upon the relative delicacy of the thermometer and since the limit of the instrument used here was about 0.25° C., in order to record a temperature rise, enough heat must have accumulated at the point of its insertion to cause .25° of temperature change. The average density and specific heat of the system would be the main factors determin-

ing the time consumed before enough heat had accumulated to cause this change. The rate of this accumulation of heat in the tissue is dependent upon the amount and rate of change in the air temperature and the *diffusivity* of the system, designated by the symbol "h^2" which equals K/CP, where "K" is the constant of thermal conductivity, "C" is the specific heat, and "P" the density (Ingersoll & Zobel, '13). The "true lag," as used in this paper, is therefore essentially invariable, at least within the medium temperature limits and the usual liquid water content of the tissues. In many of the older papers on this subject, however, the "lag" periods reported were extremely variable and irregular from day to day and over longer stretches of time. This was due partly to the method of determining the "lag," and partly to the unrecognized thermostatic factors.

It has already been noted that the intersection points of the air-temperature line with the tree-temperature lines are most important in the temperature curves, since they indicate usually momentary identical temperatures. These intersection points, which are here called *iso-thermal nodes,* have seldom been noted heretofore in the numerical data of this subject, and their significance has therefore been overlooked. It will be evident from an examination of the various temperature graphs during medium temperatures that the period from the air-temperature maximum to the following iso-thermal node was very irregular. This was influenced, first, by the rate of rise of the air temperature to the maximum, which therefore affected the rate of rise in the tree temperatures. Second, the length of the maximum period also influenced the rate and length of the rise in the tree temperatures, as well as helping to determine directly the length of time from the air maximum to the intersection. Since in most former records the length of this maximum period was undetermined, its effect on "lag" was entirely ignored. Third, the rate of decline in the air temperature prior to the intersection greatly influenced the apparent "lag" period. In general, a slow decline postponed the time of intersection of the lines, sometimes by many hours, and

a rapid decline greatly shortened this time. Now, since the maximum tree temperatures must occur *at* or *after* the intersections it is evident that the "apparent lag" between air and tree maxima must be an extremely variable quantity. Fourth, the rate of decline in the air temperature subsequent to the intersection caused variations in the length of time between the intersection and the maximum in the tree temperatures. This was influenced largely by the diffusivity of the tissues, since loss of heat by the tree could now take place in proportion to the speed of decline in the air temperature.

Analogous considerations demonstrate that the "apparent lag" between the air and tree minima also is necessarily very irregular. It has been unexplained in former investigations, due largely to incomplete data and a lack of recognition of the iso-thermal nodes. The two other factors, however, which in even greater measure and in a more important manner influence the lengths of "apparent lag," are: first, the adjustment period at the zero line, and, second, the thermostatic cooling of the tissues.

In most of the periods of declining air temperature in which the tree temperatures fell below 0° C., the tree-temperature minima were delayed by the long zero-adjustment period until many hours after the beginning of the air minima. In a few cases, notably that of January 28, 1934, a rapid decline in air temperature carried the tree temperatures below the zero line, and the tree minima were delayed due to adjustments gradually made while the tree temperatures were dropping. In a similar fashion, the tree temperature maxima, following a rise in air temperature which carried the tree temperatures above zero, were usually attained many hours after the air maximum, and in many instances the air temperature had several maxima and minima which were not even registered in the tree temperatures. This delay and frequent lack of registering of maxima were associated with the long zero-adjustment period which greatly modified the usual somewhat rhythmic rise and fall in the tree temperatures associated with the usual daily rhythm of air temperatures.

The effect of the thermostatic cooling upon lag was shown in the extreme form in July, 1934, when the low tree temperatures and the high air temperatures usually exactly coincided (and vice versa). The apparent rhythmic lag of approximately 12 hours was then entirely false, since the tree minima and maxima had no relationship to the preceding air minima and maxima respectively, as demonstrated in a former section of this paper. In less extreme cases, as during the latter part of July, 1930, the minimum period in the tree center partly coincided with the air-temperature maximum and vice versa. This condition in part obliterated the "apparent lag" period by substituting more or less of the false "apparent lag"; in other words, the tree minima, due to preceding air minima, merged more or less completely with the minima due to the thermostatic cooling action. Likewise, the preceding air maxima caused a rise in the tree temperature which merged with the rise associated with the decreasing thermostatic cooling action, and the apparent lag period was somewhat extended.[1]

FACTORS AFFECTING TREE TEMPERATURES

As was early recognized by plant physiologists, the atmosphere and direct insolation are the main sources of heat for the plant. Many attempts were made in the early days of the subject to demonstrate elevated temperatures of the embryonic regions of the stem associated with respirational activity, but few satisfactory results were obtained because of the masking effect of the rapid and excessive changes due to the outside environment. In the course of these investigations experimenters became greatly impressed with the rhythmic alternations of temperatures in the tree, apparently following more or less regularly those of the air. Many of the investigators recorded considerable deviations of the tree temperatures from those of the air, but were usually content to point out that the mean temperatures of the tree and of the air ran parallel. From the present records the importance of the air temperature as the main factor in determining directly and also indirectly the tree

[1] Another type of "false apparent lag" has been described in a preceding section.

temperature is evident. However, the factors influencing the diffusion of heat through the tissues, which is a basic physical phenomenon, must be clearly defined in order to interpret the various reactions indicated in the graph-records.

The order of magnitude of the thermal conductivity of wood is indicated by that of pine, which at 15° C. and perpendicular to the face is given as $0.361\ \lambda \times 10^{-3}$, while that of water at 12° C. is $1.36\ \lambda \times 10^{-3}$.[1] Hence the heat conductivity of the tree trunk would tend to increase or decrease (directly) with an increasing or decreasing proportion of water. As indicated later, concurrent with a decreasing water content there is an increasing amount of water vapor, and since its thermal conductivity is less than that of water (e.g. at 46° C., $4.58\ \lambda \times 10^{-5}$) the rate of heat transfer in the entire system would be further reduced by this factor. Under the high transpiration conditions of the summer the center temperature tended to respond less readily to changes in air temperature than under more moderate conditions. In light of the above, this may be partly accounted for by a net loss of water from the tissues, resulting in a decrease in heat conductivity. That there is a tendency toward a decreasing water content of trees as the transpiration rate increases has been demonstrated by various investigators (MacDougal, Overton & Smith, '29), and a study of the various patterns of water distribution in tree trunks at different seasons points toward the general conclusion that there are sharp differences in seasonal distribution and quantities of water in tree trunks (Craib, '18–'23).

Since the specific heat of ice at −10° C. is approximately half that of water at 0° C. (0.48 vs. 1.0087) the reactions of the tree temperatures to subfreezing air temperatures would tend to be more rapid when the water in the tissue is frozen than when liquid. Moreover, the heat conductivity of ice is more than quadruple that of water, or about $5.7\ \lambda \times 10^{-3}$. This physical factor also would tend to increase the speed of reaction of tree temperatures to low air temperatures as compared with the reaction at temperatures above zero. While it is not possible

[1] Physical data from Lange ('37).

at present to determine from the records the relative quantitative effects of these factors they must be considered in any attempt at a complete analysis of the factors concerned. In general, it has already been shown that the ratio between the increase or decrease in atmospheric heat and the increase or decrease in the center temperature is higher at higher temperatures and lower at lower temperatures. This must be ascribed mainly to the thermostatic cooling at higher temperatures. However, these heat-transmission factors under extreme conditions may be sufficiently important to affect noticeably the general result, as would be indicated by the fact that when the tree was at sub-zero temperatures the ratio air-temperature change/tree-temperature change was unusually low, even reaching the theoretical ratio of 1:1 as cited elsewhere. This contrasts somewhat sharply with the usual ratio at temperatures above zero when there was little thermostatic cooling, and indicates less heat absorption and more rapid heat transmission at sub-zero than at supra-zero temperatures. During the winter sub-zero periods the tree-temperature lines were more often superimposed and also more closely followed the air-temperature line in its wanderings than during early spring and late fall supra-zero periods. This general observation may be explained mainly by the recognition of these physical factors.

In a consideration of the phenomena which have been heretofore included in the phrase "zero-line adjustment," it is clear that at or just below zero, because of the latent heat of fusion of ice, heat is steadily given off as ice formation proceeds. The steady temperature at or near the zero line is thus maintained until ice formation is complete, and a continuance of an air temperature below that of the tree would cause a lowering of the tree temperature. The reverse process would take place during the crossing of the zero line concurrent with the rise of temperature. The following data seem to substantiate this concept. During the period, January 29–February 6, 1932, the center temperature line held at about -1.5° C. almost steadily, although the air temperature line was above zero for

3 days or more. However, the number of degree-hours below zero during the first cold spell was about 327, while during this first warm spell, which did not carry the temperature of the tree center above zero, it was only about 244. That this use of degree-hour units is a valid criterion is evidenced by the fact that for the entire period the total degree-hours below zero (421) just about equaled the number above zero (432), the period beginning at the time that the center temperature line crossed the zero line on its way down and ending when it recrossed the zero line.

The relatively long period during which the temperature of the tree hangs at about 0° C., even when the outside temperature is steadily dropping, may possibly be associated with the phenomenon of change of "free water" to "bound water." Newton and Gortner ('22) show that winter hardy wheat changes its free- and bound-water relationship at low temperatures, and such changes may well occur during this transition period in the tree. Gortner ('37) states that "by bound water we mean water molecules which have been so reduced in activity that they are not oriented into the crystal lattice pattern, characteristic of ice, when exposed to low temperature," and he evidently considers the binding of water as an adsorption process (Gortner, '38) which, as is well known, evolves large quantities of heat. It may then be possible that more or less of the heat evidently evolved in this "adjustment" period is derived from this source. Moreover, it has already been shown that even when the air temperature declines so rapidly that the tree temperatures are carried past the zero point an evolution of heat can still be demonstrated, proving that the adjustment process still takes place. Whether or not super-cooling occurs under these circumstances cannot yet be definitely proven, but it is entirely possible. Since this phenomenon is facilitated by the absence of active liquid movement (Luyet & Hadapp, '38) and the whole mass of water in a tree trunk is divided by the cell walls and membranes into numerous partially immobilized small units, the conditions for super-cooling would be especially favorable. The influence of the higher

osmotic concentration of the biological fluids on the freezing point during the zero-adjustment period is shown by the fact that the temperature during this time was from -0.50 to -1.50° C. instead of 0° C., with the lower temperature predominating when the temperature was on the decline.

SOIL TEMPERATURE

Several investigators have maintained the hypothesis that the temperature of the ascending soil water caused tree temperatures above or below those of the air. It was pointed out that if the transpiration stream had a different temperature from that of the air it would tend to modify the effect of the air temperature by constantly giving off or taking up heat. In some cases soil temperatures were correlated with tree temperature in substantiation of the hypothesis. Hartig ('73), in his table II, shows that a cut, living log containing water accumulated heat in the direct sunlight, while a standing transpiring tree (oak) under similar conditions, even at 4 cm. deep, definitely cooled not only to a temperature below that of the cut log but also in general below the air temperature. The cooling action could be seen in a shaded location also, although it was not so great. The cumulative heating of the log in the sun was marked, especially at the 4 cm. depth. Selected data are given in table XV.

TABLE XV

DATA ASSEMBLED FROM TH. HARTIG

Time	Outside sun temp. rise or loss	Log temp. rise or loss	Tree temp. rise or loss
6–8 a. m.	+8.2° C.	+3.8° C.	-0.3° C.
8–10 a. m.	+12.3° C.	+6.2° C.	+1.7° C.
10–12 a. m.	+0.4° C.	+6.5° C.	+1.3° C.
12–2 p. m.	+1.6° C.	+2.3° C.	+1.2° C.
2–4 p. m.	+1.0° C.	+2.0° C.	+1.5° C.
4–6 p. m.	-2.6° C.	-2.3° C.	+1.0° C.
6–8 p. m.	-5.8° C.	-4.0° C.	+1.0° C.

The air temperature (in shade) also showed a decline from 4 to 6 and 6 to 8 p. m.

Several items of interest appear in this table: (1) The manifest cooling action in the transpiring tree which held the temperature rise to less than 8° C. as contrasted with rise in the log temperature of nearly 21° C; (2) the slower rise in the log temperature as compared with that of the outside, probably because of the high specific heat of water; (3) the continued rise of temperature in the tree due to the fact that the outside temperature, although declining, was still above that of the tree and contributing heat to it; (4) the rise in temperature and accumulation of heat in the water-containing, but essentially non-transpiring log. This independent demonstration of cooling action, ascribed by Hartig to cool soil water, is of special interest, since the data were gathered from a study of a different species growing under different climatic conditions. If in the present study the cooler temperature in the tree had been due to cool water ascending from the lower cool regions of the soil, there should be specific evidence in the records. Cool water, at its maximum speed of flow, passing through the stem for one or more hours, should have somewhat reduced the tree temperature during the extended periods of maximum air temperature. However, at no time is there evidence that this took place. Moreover, there is no evidence that during the night a cooling of the tree tissues occurred due to cool water from the ground, since usually when the air temperature was at its minimum, the maximum center temperature had been reached and maintained. The only possible evidence in favor of the cooling action of soil water is that early in the morning, before the sharp rise in air temperature, the center temperature sometimes made a slight drop before the sharper drop of the day. However, this can be explained by the same factors that account for the major cooling action as discussed later.

Furthermore, the cooling effects reported here could not be considered as due to the temperature of the soil water for the following four reasons: First, the greatest cooling was in the center where, it is universally agreed, there is the least conduction of water and where gases predominate. Second, when the temperature of the air began to drop that of the center be-

gan to rise, while that of the cambium usually accelerated its rise. This change of tree-center temperature could hardly be ascribed to a change of temperature in the soil water, nor to its warming-up due to slower conduction, since the center was affected as soon as the conducting region. Third, the amount of change in the cambium temperature was somewhat proportional to that of air temperature and less than that of the tree center, whereas it should have been more if due to a change in the temperature of the transpiration stream. Fourth, the beginnings of these responses were essentially instantaneous, which could not have been true if they had been dependent upon the rise of the water from the soil through 30 to 40 feet of vascular tissue. Finally, the marked cooling action during July, 1934, could not have been associated with the passage of cool soil water through the trunk, as evidenced by a comparison of the records of corresponding dates of other years. When, for example, as shown by the continuous chart record during much of July and early August, 1932, the air temperature varied slightly, the temperatures of the cambium and of the center varied mainly between 25 and 30° C. In July, 1934, during the prolonged hot period the tree minima were often close to 15° C. Manifestly, the soil temperature in the same location could not have been approximately 15° C. in 1934, and 25° C. in the cooler year of 1932. While there is thus no evidence that the temperature of the soil water is the main factor in controlling the temperature of the tree, it seems probable that it is a contributing factor in modifying the final temperature.

The same general statement applies, in some degree, to the belief that the warmer soil temperature of winter might be a source of heat which flows upward through the root system into the tree trunk, thus helping to maintain a temperature in the tree trunk somewhat higher than that of its surroundings. Such a hypothesis has no basis in direct observation.

STRETCHING OF WATER COLUMNS AND VAPORIZATION

The presence of water vapor in the tissues of the tree has long been taken for granted, and Scheit and von Höhnel, by

various ingenious experiments, demonstrated the probability of water vapor in the tracheae. Nevertheless the corollary of this concept, namely, that by the absorption of heat in the process of vaporization the tissues would necessarily be cooled, has apparently not been given due consideration. There has been much discussion concerning the presence or absence of air bubbles in intact tracheae of the hydrostatic system, but at least a certain amount of water vapor would necessarily be present in such bubbles. The amount of vaporization into these bubbles would increase with an increasing negative pressure, resulting in an increased absorption of heat from the surrounding tissues. Vaporization into the pneumatic system would likewise cool the tissues. If, as is postulated in the traction-cohesion theory of water transfer, the water columns become stretched and if this liquid acts similarly to other substances under stress, it would be cooled in accord with the well-known physical principle that substances which expand upon heating absorb heat in the process of stretching. Thus two possible physical processes exist which seem to fulfill the general known or postulated conditions in the tree and which separately or together may account for the cooling action demonstrated in these studies. A careful consideration of the detailed records and of the various special conditions involved should give some indications whether one or the other of these physical processes is to be given preference in the formulation of a theory.

The general considerations involving the relationships between the several factors under study here have been given in considerable detail by MacDougal, Overton and Smith ('29). Certain of their conclusions which have important bearings upon this problem are given here.

"A cohesive meshwork of sap occupying portions of all untylosed annual layers of these trees.

"The cohesive columns of water occupying the tracheids and vessels are in a state of tension set up by evaporation from the exposed walls of cells adjoining intercellular spaces of leaves.

"Dendrographic studies made show that the pull set up by water-loss from such surfaces causes daily variations in size of intact stems and trunks, owing to an increase and decrease of the tension.

"Pressures and suctions on the gaseous system within the trunk are readily transmitted vertically for distances many times the length of the vessels. Tangential transmission of suctions and pressures is at a very slow rate, and is even slower in a radial direction.

"The relative volumes of the hydrostatic and pneumatic systems within the tree are subject to variation during the course of the season. Specific conducting elements may at one time be partially or wholly filled with gas, and at another time filled with water.

"Tensions in the pneumatic system may vary from something less than half an atmosphere to not more than one or two atmospheres. Tensions of the hydrostatic system may vary from a compression or positive pressure to a suction or pull of one to two hundred atmospheres."

It would appear then from the studies of MacDougal and his associates that the increased foliar transpiration under increasing air temperature might produce two effects as related to this problem. The greatly increased tension of those water columns which remained intact would cause absorption of heat from the surrounding tissues. Moreover, vessels might be added to the pneumatic system by the breaking of their water columns, associated with an increased production of water vapor, and the extraction of heat would effect an increased cooling in the tissues. This condition of greatly stressed water columns seems to require that the greater cooling action should be at the place of greatest tension, which would be in the younger wood near the cambium zone. However, in these studies the colder area was always found to be in the tree center, whenever thermostatic conditions could be demonstrated. There seems to be no combination of circumstances in the tree trunk by which the greater cooling action could take place at an outer layer of tissue and cause a lower temperature in an inner region. Although we cannot ascribe the main cooling of the tree center directly to the stretching of water columns, at the cambium layer this might be an important, or even the major, cause. Since the cambium layer would receive much more heat than the center by conduction from the outside, it is probable that there would be a considerably greater potential cooling force there than is evident by the temperature recorded. If, on the other hand, we assume with Priestley ('32) that there is no such great tension on water columns, then

vaporization of water in the tissues appears to be the only adequate physical principle to account for the notable cooling action with its immediate response to changes in air temperature.

As this discussion indicates, the conditions necessarily postulated under either hypothesis would lead to some vaporization. This process absorbs a large amount of heat (584.9 gram-calories per gram at 20° C. to 574.0 at 40° C.) from the immediate environment and cools it proportionately. The inner tissues of the tree, being somewhat insulated from the surrounding atmosphere, may attain and for some time may hold in part a temperature considerably different from that of the environment. Any conversion of water to water vapor will thus tend to cool the tissues in proportion to the amount vaporized. An advancing air temperature would usually induce a higher rate of foliar transpiration which in turn would cause a greater rate of internal vaporization. With a drop in air temperature the rate of transpiration, and with it the rate of internal vaporization, would decrease. This would result in a decrease in the cooling of the tissues and a consequent rise in temperature, due to the flow of atmospheric heat inward and possibly to a positive release of heat in the tissues through the transformation of water vapor to water.

Since there is a steady flow of heat into the tree, there must be a steady absorption of this heat, as was demonstrated by the fact that the tree temperature does not rise and may even become lower. This would mean, under the vaporization hypothesis, that vaporization must be maintained concurrently with this inward flow of heat. Since increasing transpiration leads to water deficit in the tissues, including the stem, increased space is constantly being made available for water vapor, more or less in direct proportion to the rate of transpiration. Vaporization would tend to continue until an equilibrium has been attained, but due to the changes in rates of transpiration it would not for long remain poised. It is assumed that the walls of the tracheae in the hydrostatic system are constantly moist and that whenever they are in contact with spaces in the pneumatic system vaporization proceeds as indicated above. More-

over, throughout the pneumatic system there would be a tendency for the vapor pressures to become equalized. The movement of vapor longitudinally would doubtless be very rapid, as MacDougal and his associates ('29) have demonstrated that pressures are transmitted longitudinally at relatively high rates. Imbibition in the walls and diffusion of vapor through the lumina would account for the lateral equalization. The relationships of water and water vapor to each other and to the structural units seem to provide an adequate system in which vaporization would be effective in the tree trunk. However, the question of the relationship between the foliar transpiration and vaporization in the vascular region is important. It is generally accepted in the traction-cohesion theory that transpiration causes a definite pull upon the water in the vascular elements of the leaf which is transmitted downward through the connecting vascular elements to the entire body of water in the hydrostatic system. Apparently the tendency toward rarefaction of the pneumatic system which would be induced by the tension on the hydrostatic system is partly compensated, since MacDougal and associates ('29) did not find negative pressures in the pneumatic system corresponding with those possible in the hydrostatic system. It would seem probable, in view of the sharp cooling at the tree center, that at least some, if not all, of this compensation is associated with the added production of water vapor. This might account also for the almost instantaneous inverse response of the center temperature to increase in the air temperature. On the other hand, Priestley ('32) accepts the concept of the presence of water vapor in some elements essentially throughout the vascular system, with the water columns breaking and vapor replacing the water in additional tracheae as transpiration increases. This replacing of water by vapor would cause the cooling of the tissues. Priestley's concept also definitely implies a partial rarefaction of the contents of the tracheae, which might extend rapidly for long distances throughout the vascular system until a temporary equilibrium had again become established. Hence this concept also might account for the almost instantaneous nature

of the temperature responses. The greater cooling at the tree center may be associated with a reduction in the water content there, thus leaving more space for vaporization from the inner front of the hydrostatic system.

The effect of temperature upon the water-vapor holding capacity of air is an important factor in the internal adjustments of the tree. The mass of water vapor in saturated air at 10°, 20°, and 30° C. is given as 9.398, 17.28, and 30.36 grams per cubic meter respectively, or, an increase of over 83 per cent between 10 and 20° C., and of over 75 per cent between 20 and 30° C. Hence, concurrent with a rise in temperature within the tree, in response to a rise in the environmental temperature, there would be an increase of the water-vapor capacity of the pneumatic system. This in itself would cause an increased vaporization with a corresponding abstracting of heat, thus preventing the full potential direct response of the tree temperature to changes in the environmental temperature. It would also provide for a more effective increase in internal vaporization associated with increased foliar transpiration. On the other hand, coincident with a decline in the internal tree temperature, there would be a decreased vapor capacity in the pneumatic tissue resulting in a condensation of water vapor to water with its attendant release of heat to the tissues and therefore a decrease in the cooling action. This may account largely for the fact that even when the tree was bare of foliage and the air temperature rose sharply, as from 10 to 20° C., the tree center failed to respond as rapidly or to attain as high a temperature as the air. This phenomenon is well shown in the records for February 24 and 25, and March 18 and 19, 1932, as well as in many other similar periods of the year.

The data given in this paper demonstrate an almost instantaneous influence of the air temperature upon the cooling action in the stem. The anatomical structure of the stem system in general provides an excellent channel through which such a rapid action could take place. The veins of the leaf, through the petioles and twigs, connect downward with the cone of vascular tissue of the older stems. In passing from the lower por-

tion of the stem upward the older layers of wood, one at a time, "run out," but sheathed by and connected with the younger layers. Since the foliage system as a whole is connected with all of the layers of both the hydrostatic and the pneumatic systems, its influence can reach every portion of the vascular system which is not blockaded against the fluid contents of the tubular elements. Whether we conceive of the transpirational pull acting upon the liquid contents of the hydrostatic system or upon the gaseous contents of the pneumatic system, we have an adequate channel through which this pull may act very rapidly and affect more or less every portion of the vascular tissue. As required by the data in this paper, an increased transpirational pull, induced by increased air temperature, will be transmitted rapidly through the water of the hydrostatic system to places where this system and the pneumatic system come in contact. There the water will tend to retreat into the tracheae, thus tending to increase the air space. Because this reduces the vapor tension in the air space instantaneous vaporization into the pneumatic system will take place, the amount depending directly upon the strength of the transpirational pull. It seems probable then that a considerable amount of the cooling action in the tree is associated with internal vaporization into the pneumatic system. In addition there may be a certain amount of cooling in the hydrostatic system, associated with and in direct proportion to the amount of stretching of the water columns. This physical action might under some circumstances cause the major portion of the heat absorption from the tissues of the hydrostatic system, depending upon the ability of the system to develop a continually increasing amount of stress. If the water were immobilized in the tracheae, or the transpirational pull ceased to increase and the system were then at rest, so far as additional force is concerned, there would then be no additional cooling and the temperature would begin to rise due to the inward flow of heat. This latter condition would perhaps be the main reason that the temperature of the cambium tended to rise earlier in the day than did that of the center, when the air temperature approached and held its maximum.

A second question in connection with the thermostatic action is why the cold temperature of the tree is maintained for a time and then, in immediate response to the beginning of the decline in the air temperature, begins to rise. Because of the high specific heat of water and its low thermal conductivity the layer of hydrostatic tissue acts as an excellent insulation, preventing the rapid inflow of heat to the inner tissues. This, together with such positive cooling as may take place in the hydrostatic system, would tend to hold the low temperature of the interior. When, however, the air temperature begins to drop, the transpirational pull decreases, the stressed hydrostatic system tends to reoccupy some of the pneumatic area, and vapor changes back to water, thus releasing heat. It appears then that all of the major questions associated with the thermostatic action are answered on the basis of the hypothesis discussed above.

At different times of the year and under different climatic conditions these various modifying factors differ in their influence on the tree temperatures and on the form of the curves, so that it is difficult to draw definite conclusions as to their importance except in certain of the more obvious cases. Broadly speaking, the temperature of the environment is the major factor determining the tree temperature. Certainly the major modifying influence around the zero point is the physical and physiological adjustment which takes place, while at sub-zero temperatures the tree temperatures closely follow those of the air. Under conditions of high transpiration, especially when due to high temperatures, the thermostatic cooling is the main modifying factor, and this may at times nearly cancel the effect of increasing air temperatures. During moderate temperatures thermostatic action is more or less manifest as a modifying factor, especially during the period of completely developed foliage. Throughout all of the year the form of the curve is greatly influenced by the speed of air temperature change and the lengths of the maximum and minimum air-temperature periods. It is especially important, in attempting to explain the apparent temperature responses in the tree, to locate the iso-thermal nodes and to determine the conditions before and after these points.

From time to time during the last hundred years the subject of water vapor in the vascular system of plants has been discussed in botanical contributions. The accurate, refined temperature-recording apparatus used in this study, combined with other appropriate studies, should develop important information toward an understanding of water-vapor in relation to the hydrostatic system and of its significance in water transport.

From the data presented in this paper it seems evident that the severity of temperature extremes and of temperature changes may be considerably mitigated for the plant through the zero-adjustment period and the thermostatic action. Much higher temperatures in the plant tissues certainly would occur were it not for the latter, and it may be significant that whereas temperatures capable of injuring protoplasm might readily develop from direct insolation, injury of this type seldom occurs under active transpiring conditions. In this investigation cambium temperatures were held well below 40° C., although even the shade temperatures on some of these days continued above 42° C. for several hours. At the other temperature extreme, the injurious effects of the freezing and thawing may perhaps be somewhat reduced by the long period over which the uniform temperature close to the freezing point is usually maintained.

Summary

1. Former studies of tree temperatures were inadequate because of lack of proper apparatus and of continuous observation.

2. A continuous, accurate, detailed, automatic record of air temperatures and cambium and center temperatures of a cottonwood tree was kept for about four years.

3. A typical record for one day is described; special precautions which are necessary in interpreting the records are cited; and the "degree-hour" is described.

4. A summary of certain general results shows that at about the zero point the tree temperatures usually do not follow immediately that of the air, and often do not drop below zero until

after 24 or more hours, whereas below zero as a rule they closely approximate the air temperature; at high temperatures there is a thermostatic cooling action in the tree tissue which partly or entirely counteracts the effect of the flow of heat inward; in extreme cases a temperature at about 15° C. was maintained when the air temperature was about 42° C., and the cambium was intermediate; high foliar transpiration producing a water deficit in the vascular tissues is indicated as inducing internal vaporization and consequent cooling of the center; at medium air temperatures the tree temperatures followed them, but considerably modified by thermostatic cooling and other factors.

5. A detailed examination of a number of "case studies" during the low temperature periods demonstrated that the temperature of the center has a distinctly modifying effect on that of the cambium; that after the zero-adjustment period the "lag" was for the cambium about 0.50 hour and for the center about 1.5 hours; that during the zero-adjustment period the ratio air-temperature change/tree-temperature change was high and in sub-zero weather low, even attaining the theoretical value of 1:1; that even when a rapid drop in the air temperature carried the tree temperatures across the zero-line with little "apparent lag" the internal adjustment can be demonstrated by a study of this ratio.

6. "Case studies" of high-temperature periods demonstrated that the thermostatic cooling of the tree tissues was a universal phenomenon; that this was essentially an instantaneous response to changes in air temperatures; that the cambium was kept at a lowered temperature by this action; that the tree temperature was a resultant of the flow of heat inward and of the thermostatic cooling; that from July 13 to 26, 1934, the exceptional uniform conditions produced approximately a "controlled experiment" for the study of the effects of air temperature upon those of the tree; a modified "degree-hour" method was useful in estimating these effects; that "true lag," which is the measure of the rate of flow of heat across tissues, can be distinguished from "apparent lag," which is a composite of

many factors; that "apparent lag" was essentially eliminated by the thermostatic action during this exceptional high temperature period; that direct insolation was a minor factor at this season of the year; that the "true lag" in the cambium was 0.50 hour and in the center 1.50 hours or less.

7. The main conclusions from the selected "case studies" during the medium temperature periods were that thermostatic cooling was effective in various years and essentially from the beginning of the period of full foliage, thus indicating that transpiration is the means by which air temperatures affect thermostatic cooling; that the "true lag" periods were here usually the same as for high- and low-temperature periods; that direct insolation was a factor in the cambium temperature at times but at most a minor factor which could not be clearly detected in the center temperature.

8. The problem of "lag" throughout the records is discussed. It is shown that the intersection points of the air-temperature line with the tree-temperature lines, which are denominated "iso-thermal nodes," are important in analyzing the records and in determining the reasons for the "apparent lag" of the tree temperatures behind the air temperatures. The "lag" periods of older writers were of very irregular length due in part to incomplete records and in part to an apparent misconception of the factors affecting lag.

9. While the air temperature is the major factor in determining the broad limits of tree temperatures, its effect is greatly modified by various factors, some of which were discussed in preceding sections. In addition to those, the following are considered: the thermal conductivity of wood substance and of water and of water vapor; the different specific heats of water and of ice; the latent heat of fusion of ice; "free" and "bound" water; and the osmotic composition of the cell sap. The temperature of the soil water apparently had little effect in determining these tree temperatures, and it is doubtful if it is ever an important factor. This conclusion applies also to the flow of heat from the soil through the tree tissues.

10. The stretching of water columns and vaporization within

the tissues, both due mainly to foliar transpiration, are suggested as the main, more or less cooperating, causes of thermostatic cooling. These are considered both in light of the factual physiological and anatomical evidences and of various theories. In general, it appears that stressing of water columns may be important in the young wood layers near the cambium; and the vaporization process especially important throughout the pneumatic system, whether permanent or temporary. The difference in the vapor capacity of the air of the pneumatic tissue, due to differences of temperature, causes a direct thermostatic action, as well as having a modifying effect when the transpiration rate is changing. The hypothesis suggested is believed to be adequate and no other at present seems to fit the known facts.

11. Some suggestions are made as to the possible relative importance of the main factors in influencing tree temperatures; the special value of this method of investigation as applied to certain other important problems in tree physiology; and the possible protective benefits which the plant may derive from the temperature adjustments studied in this paper.

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[1] A complete historical summary and review of the work on tree temperatures is in the course of preparation, and only a few, selected, pertinent references are given here.

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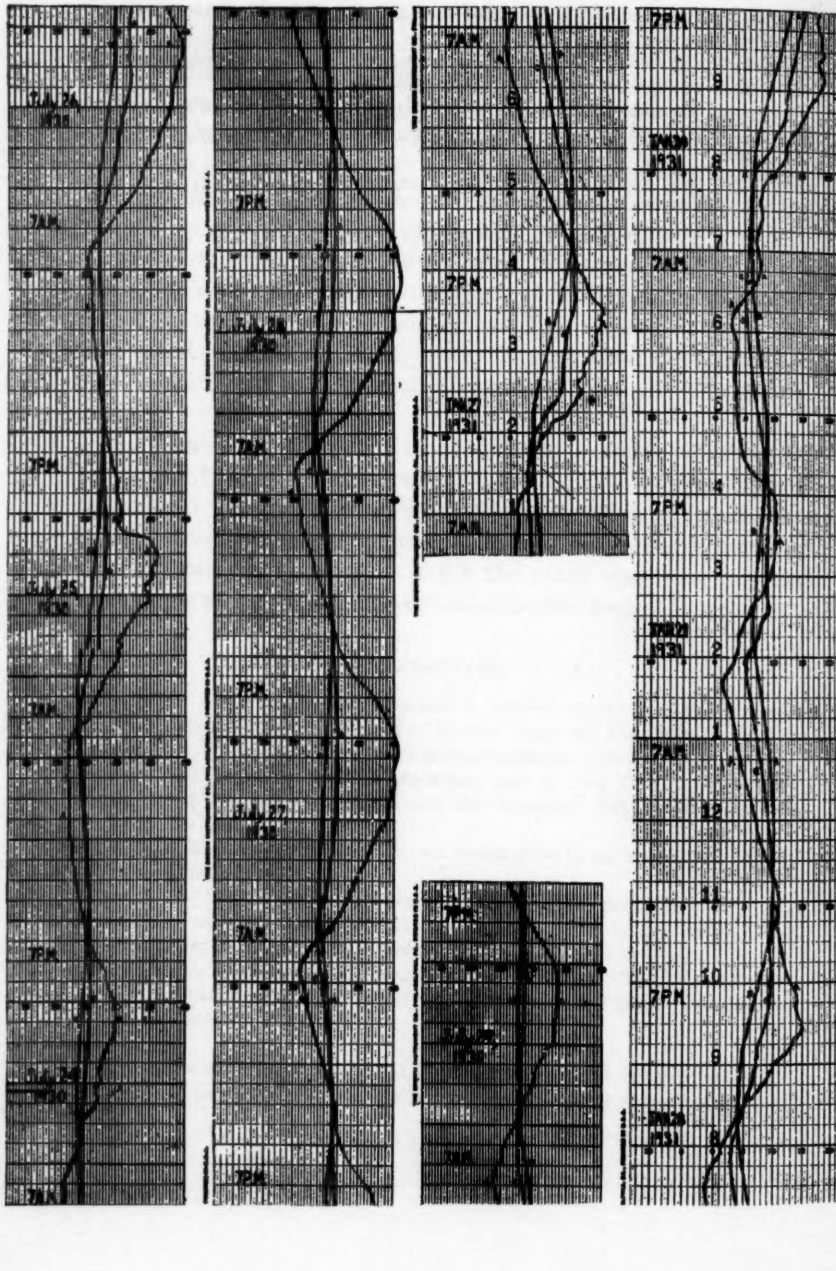
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JAN27
1931
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1931
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JAN29
1931
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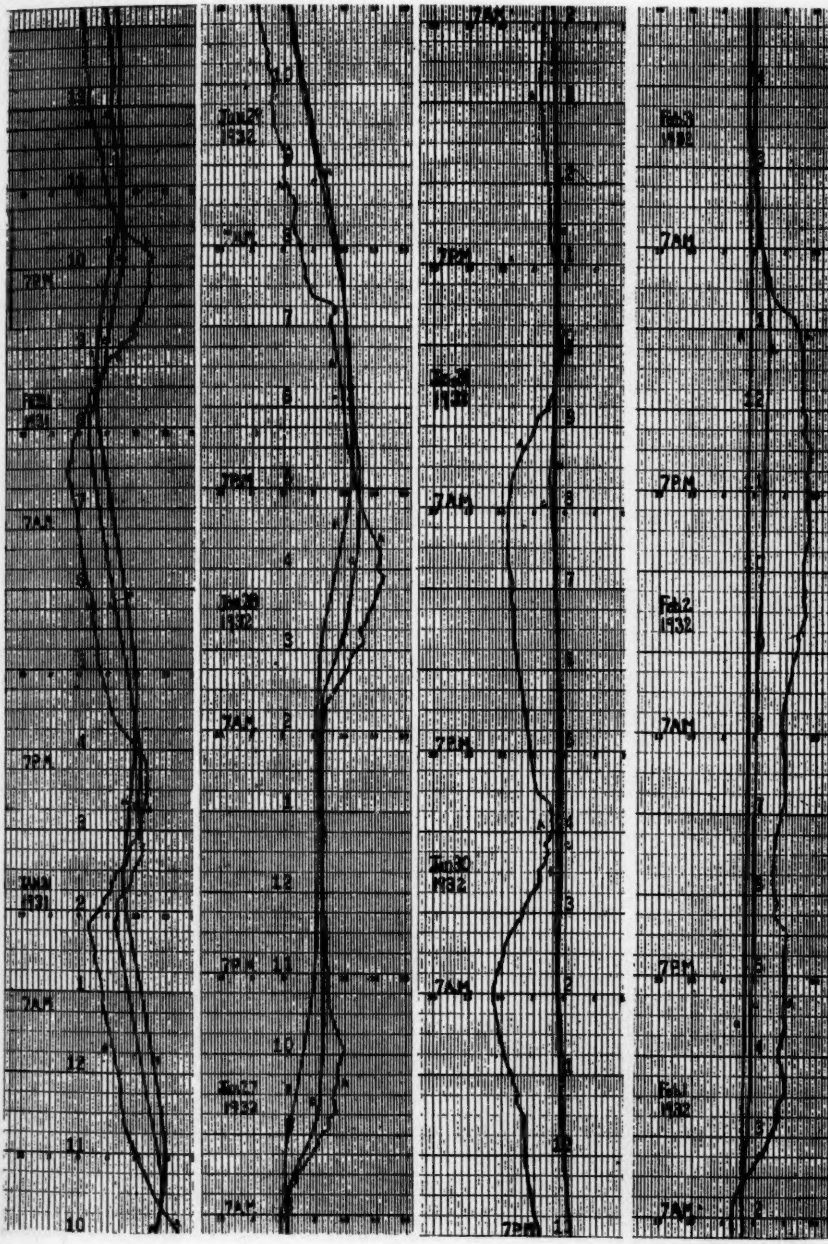
JAN28
1931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1932
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Jan 27
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Jan 31
1932
7AM
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Feb 3
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Feb 2
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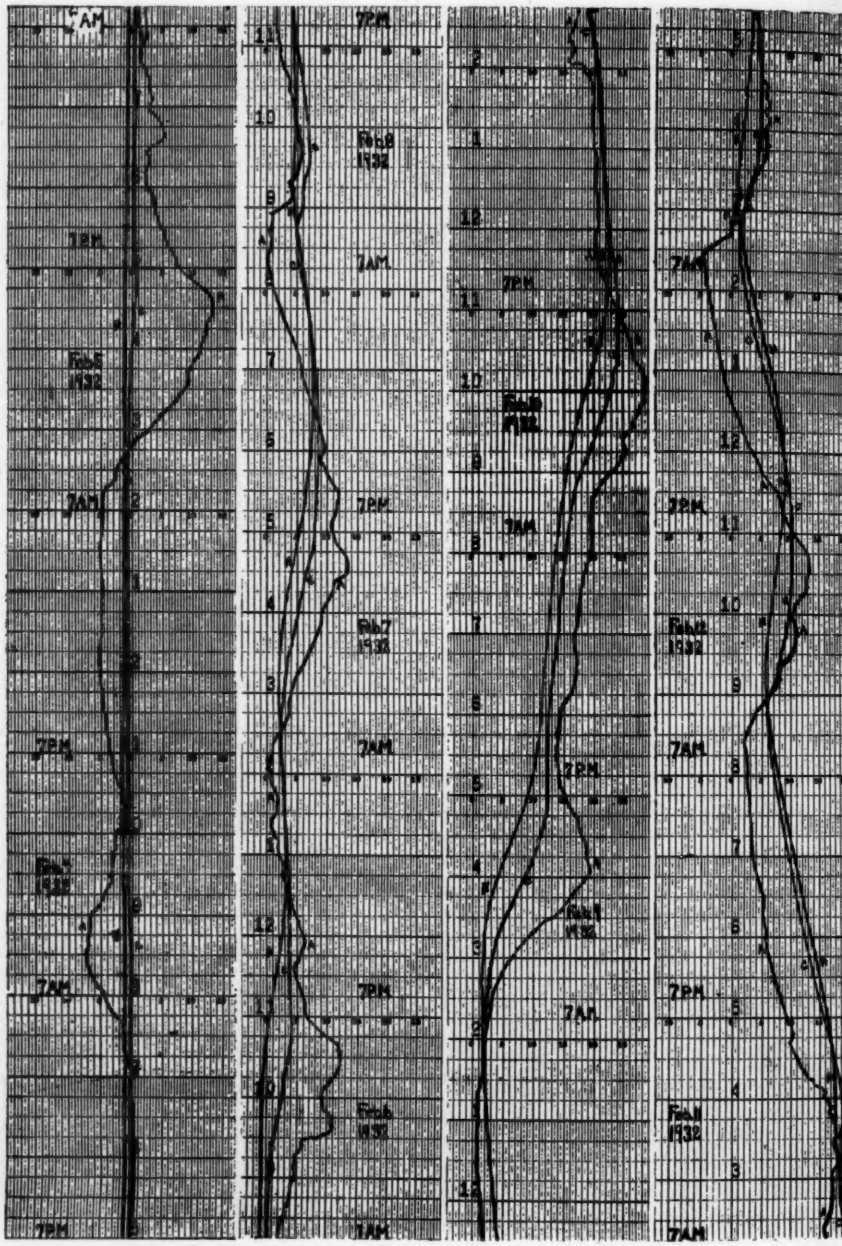
Feb 1
1932
7AM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Feb 7
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Feb 12
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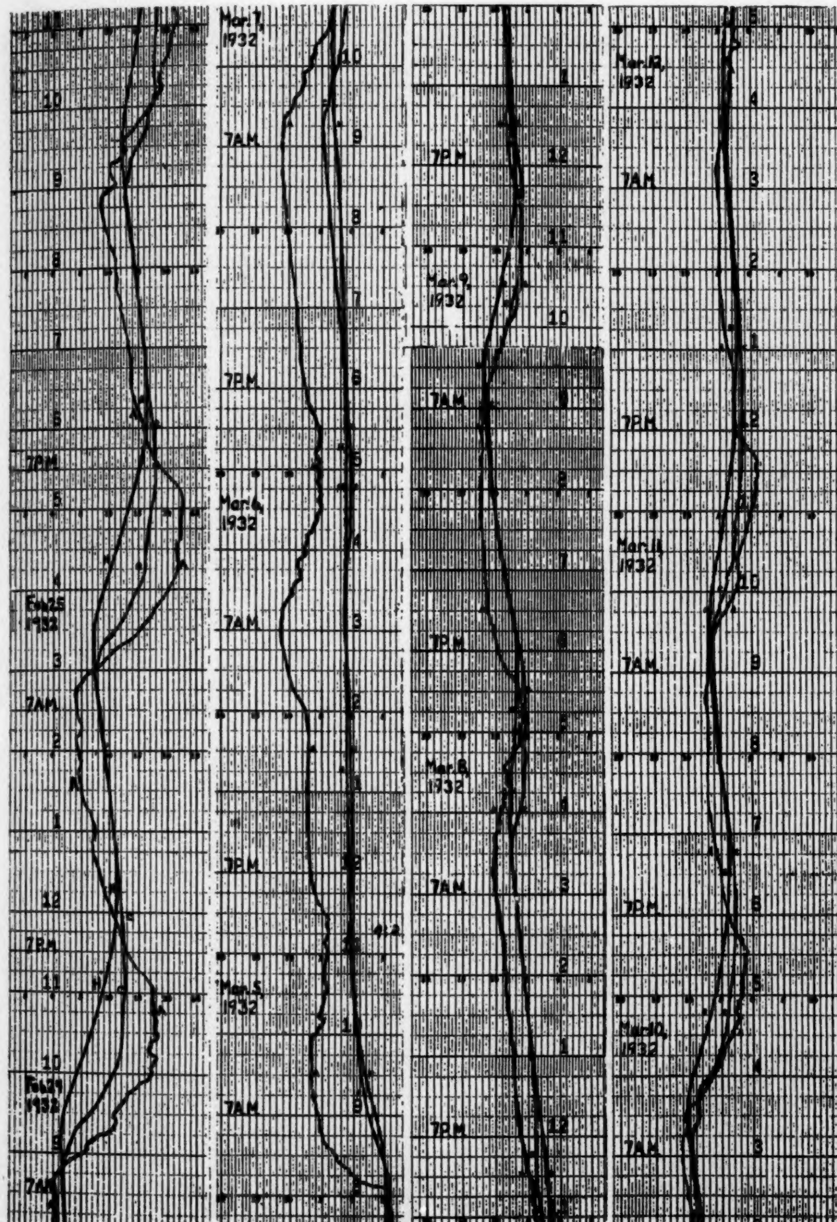
Feb 11
1932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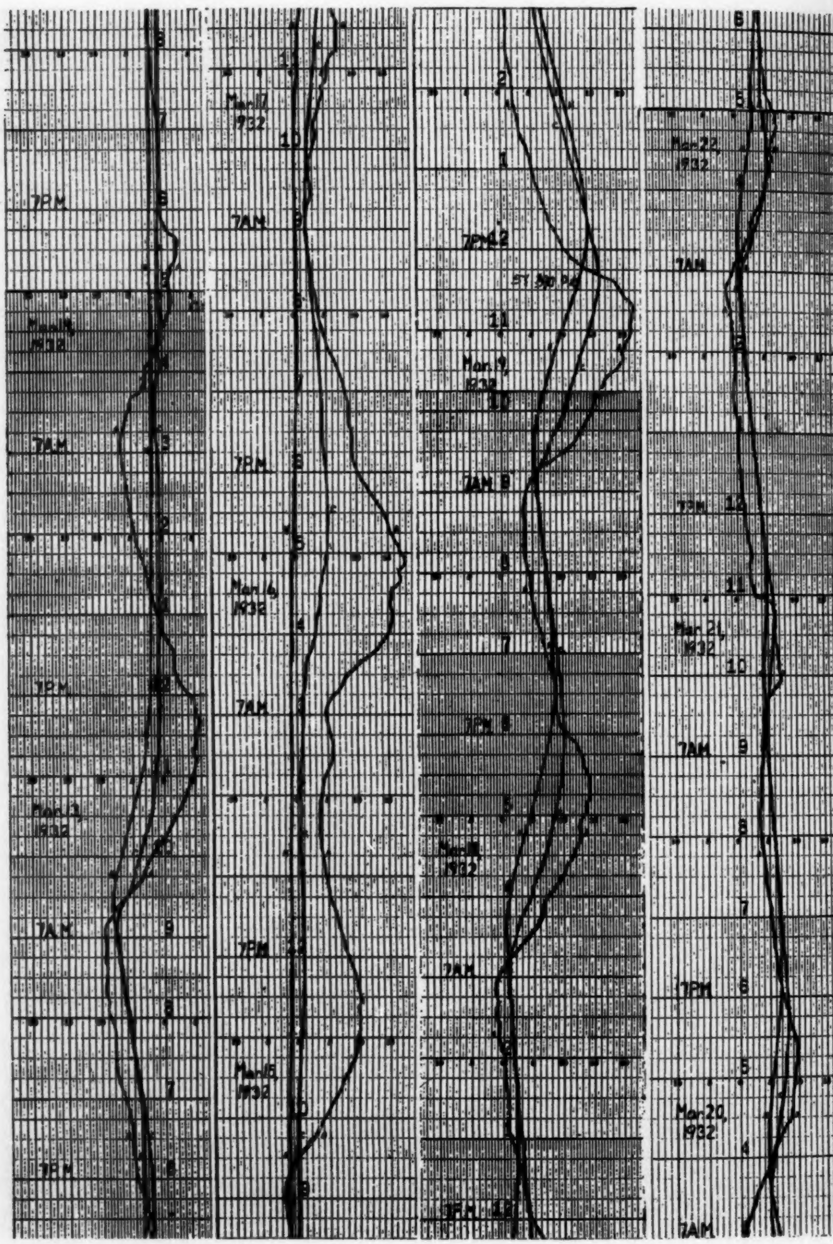
Mar.10, 1932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Mar. 20, 1932
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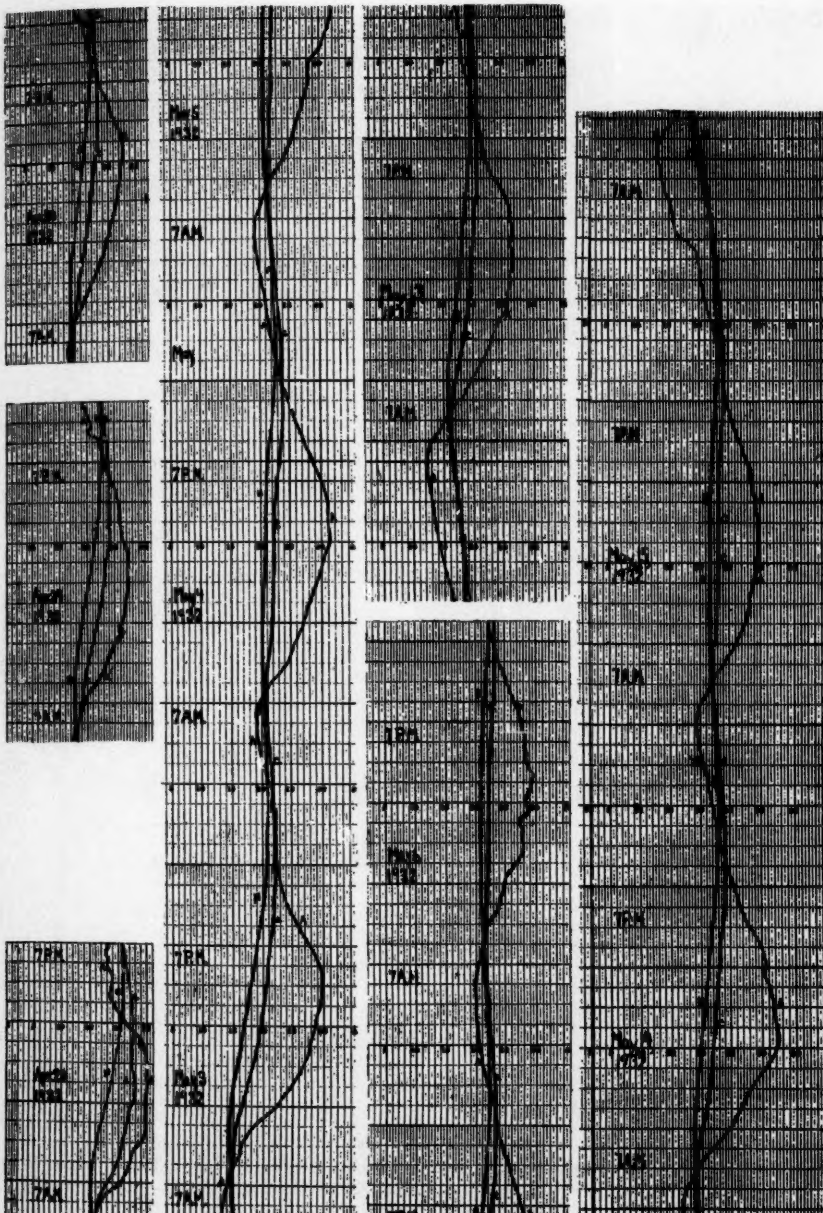

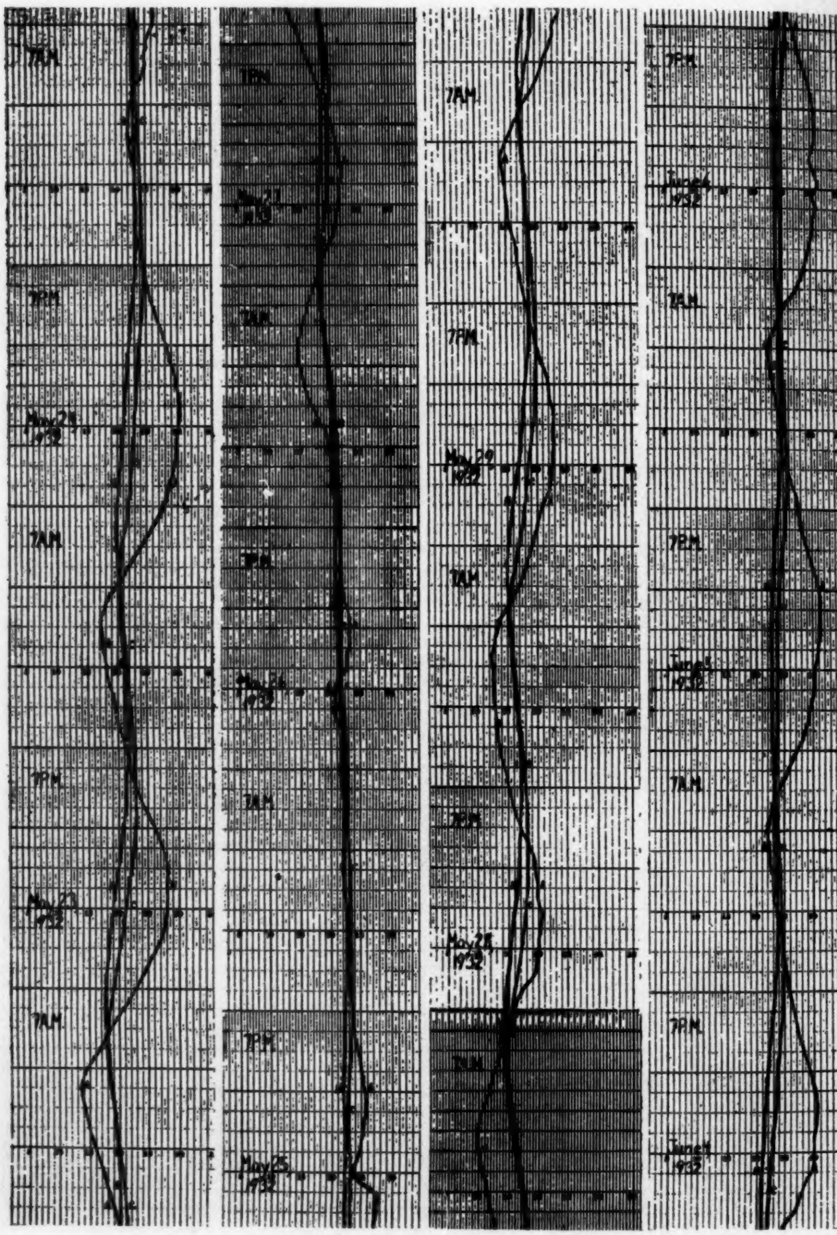
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May 29
1932
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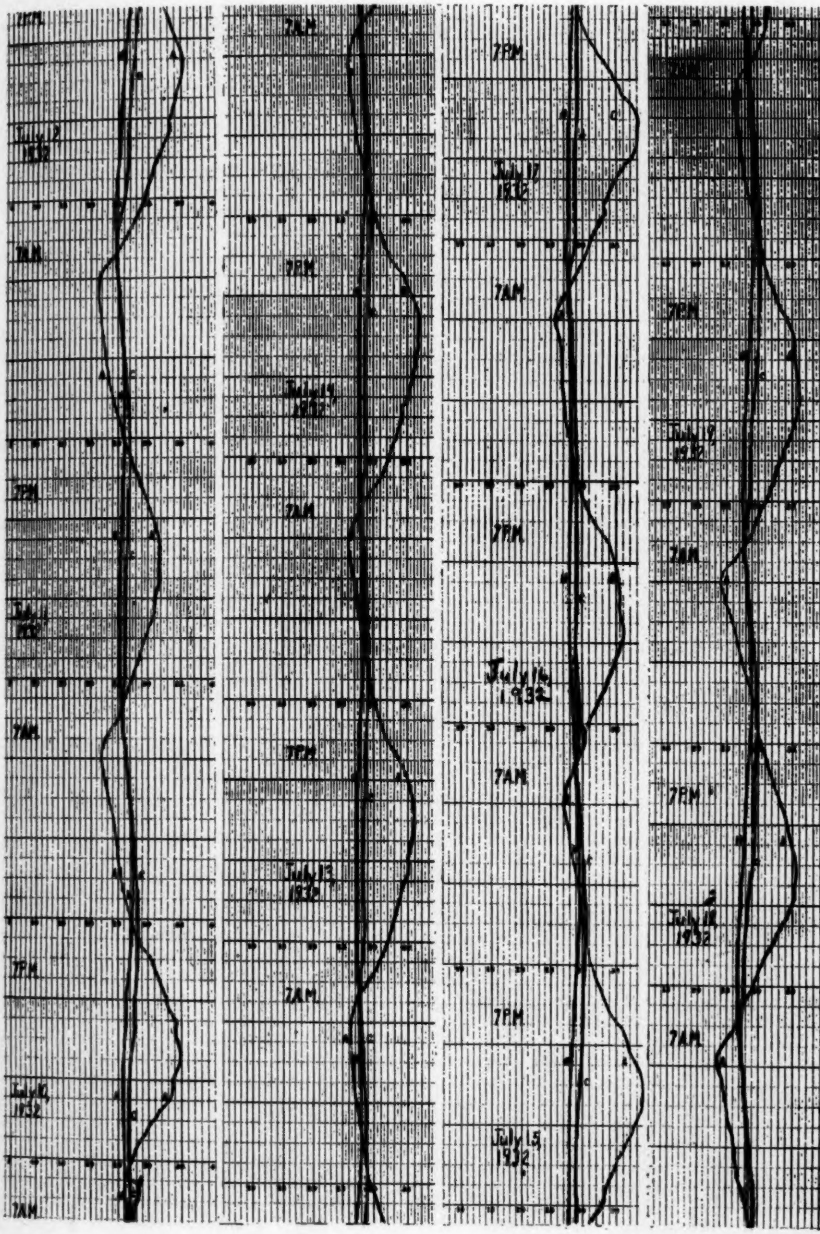
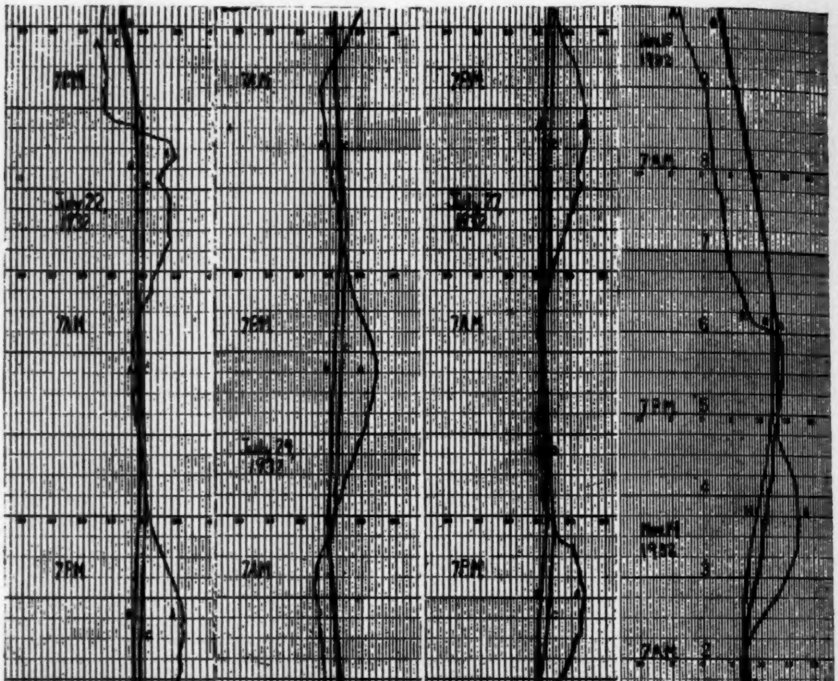
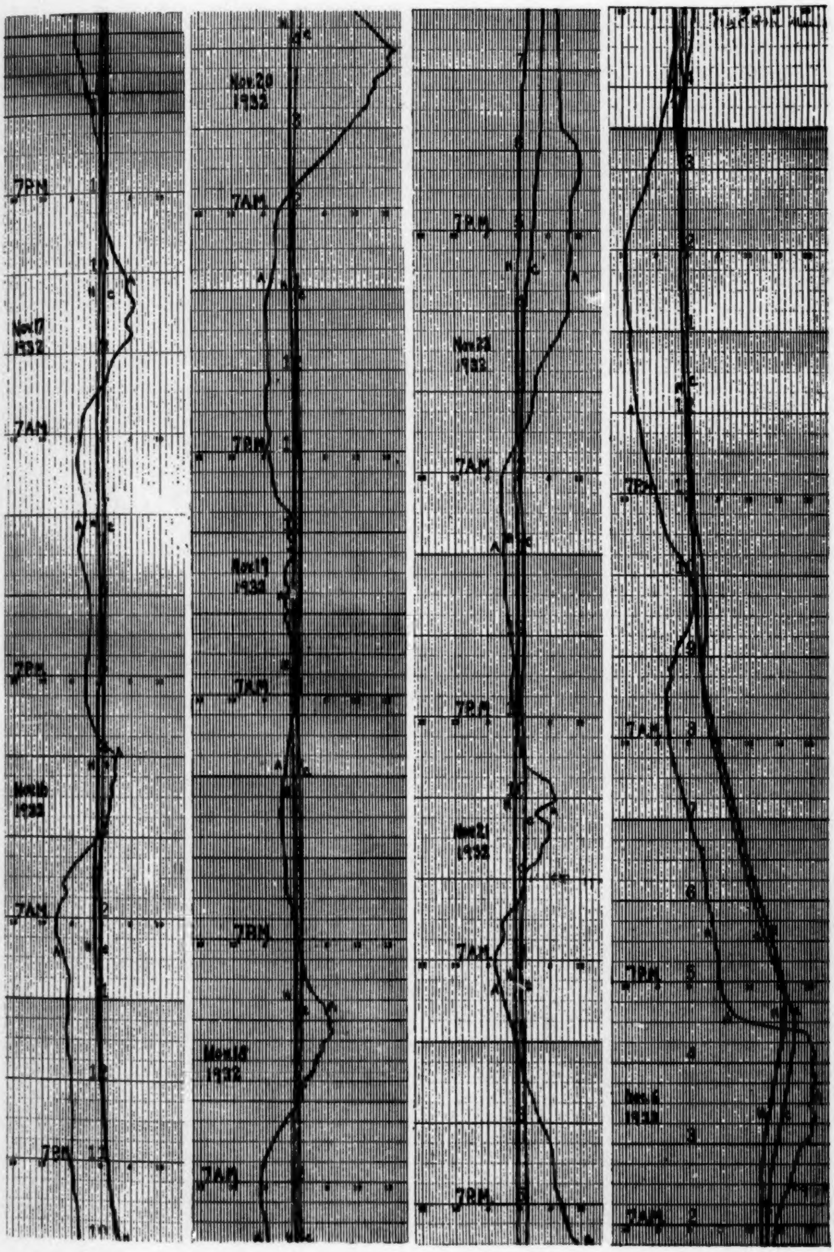
1932



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1932
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Nov 17
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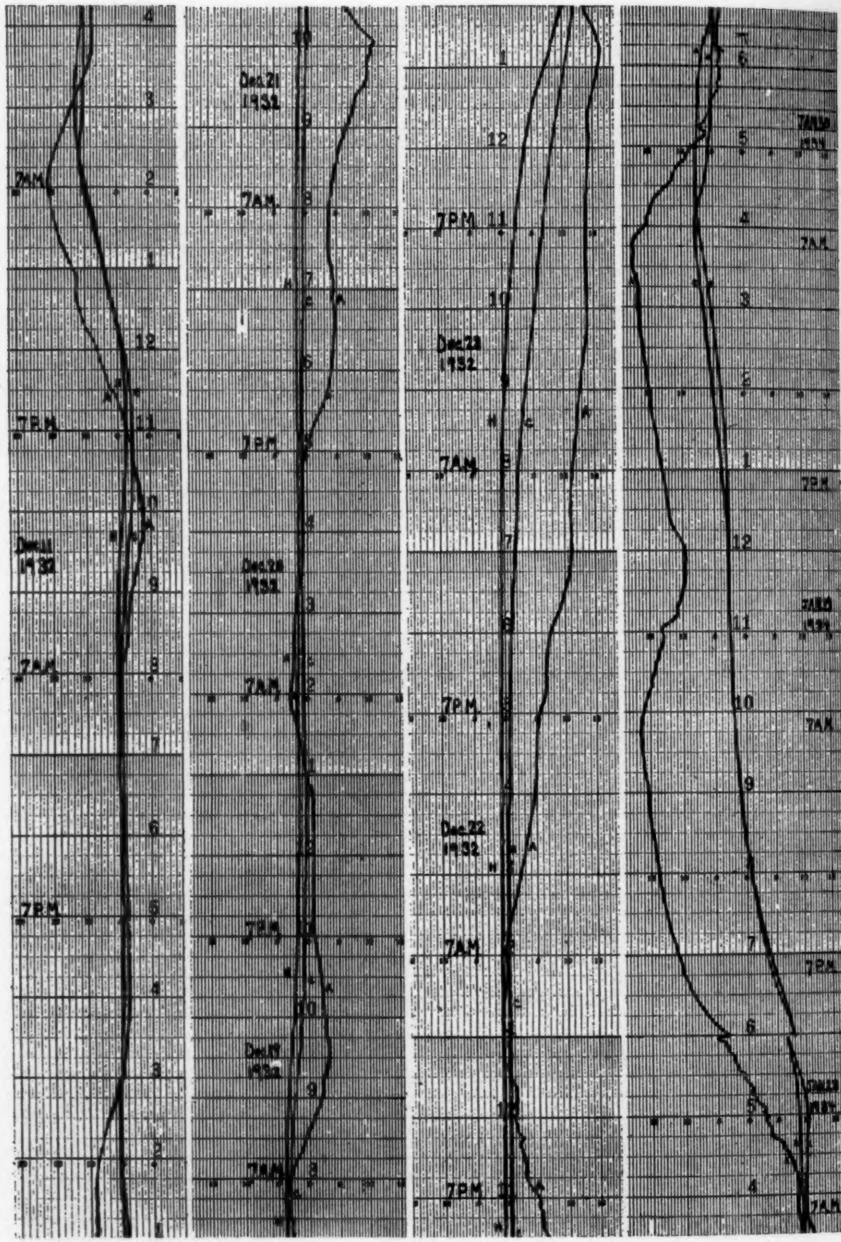
Nov 19
1932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Dec.20
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Dec.23
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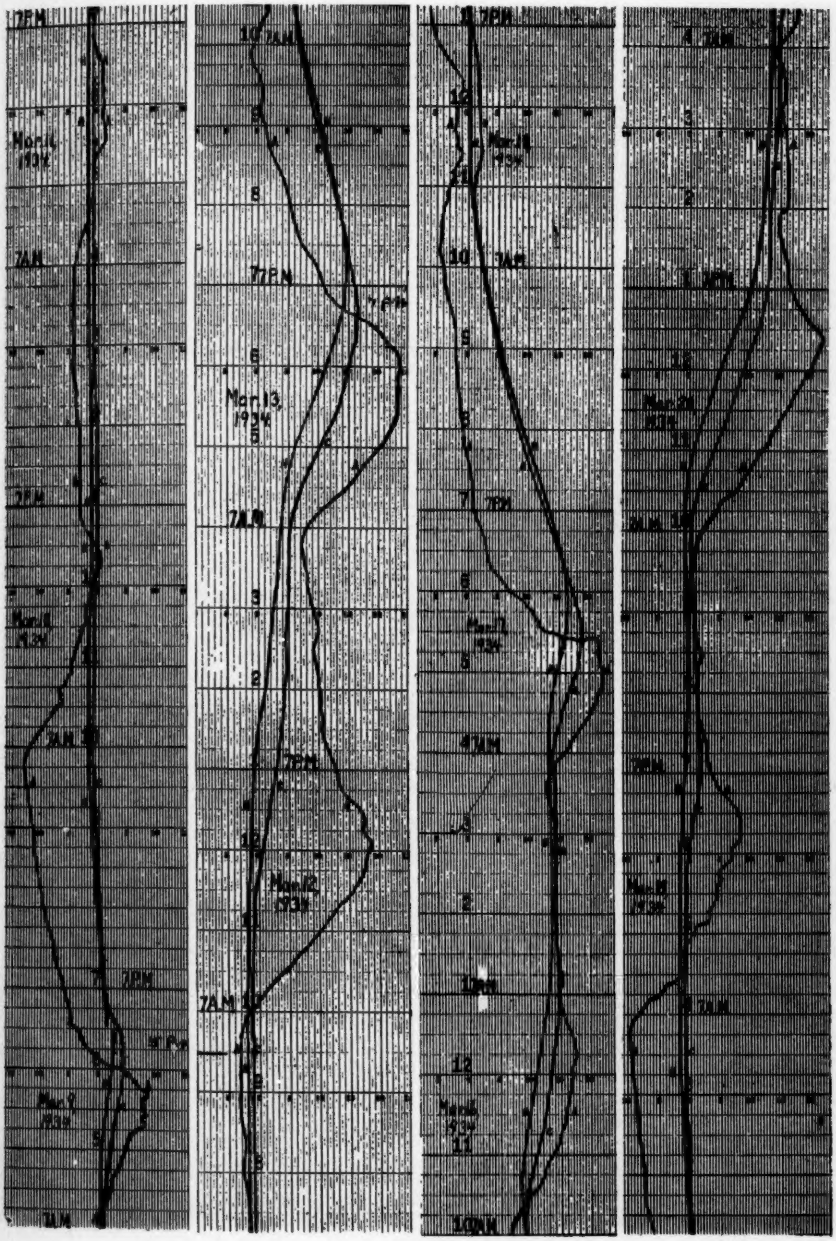
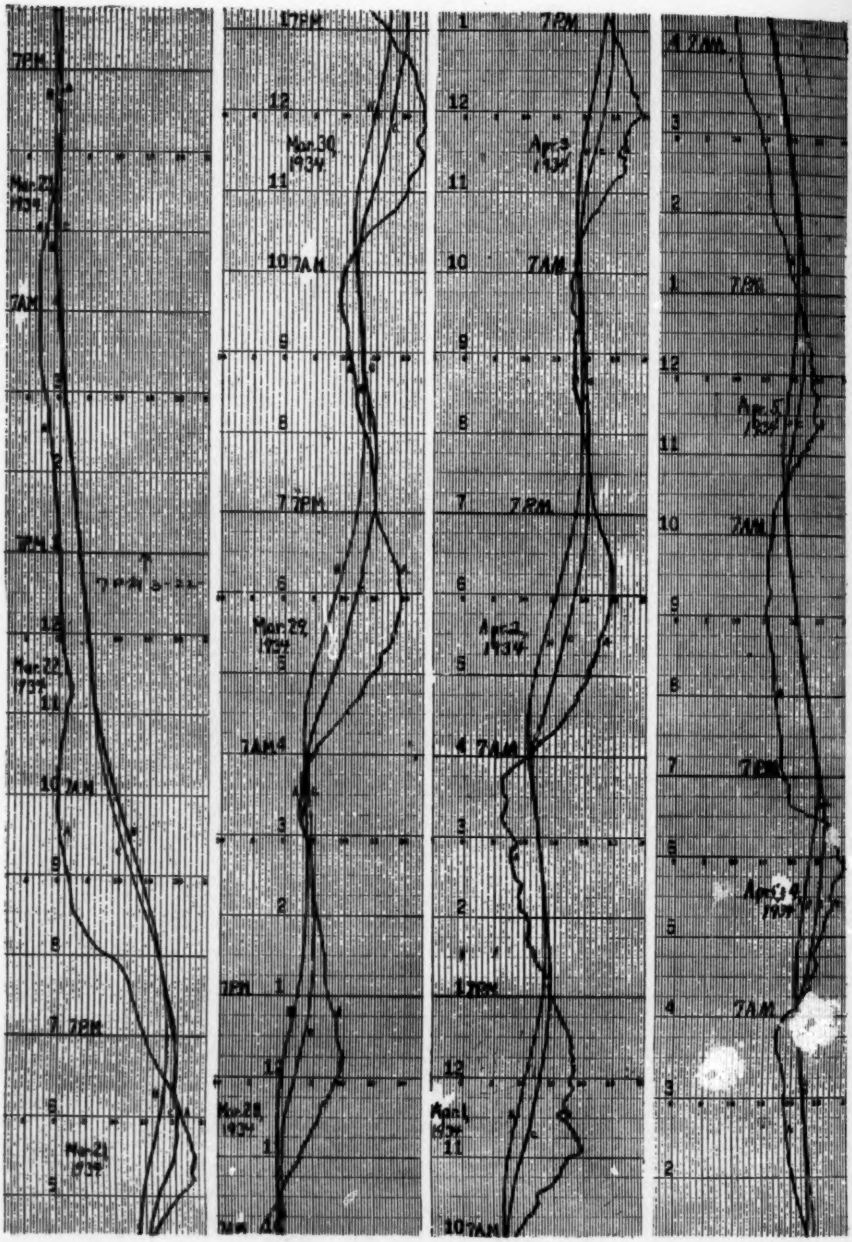
Dec.22
1932
7AM
7PM

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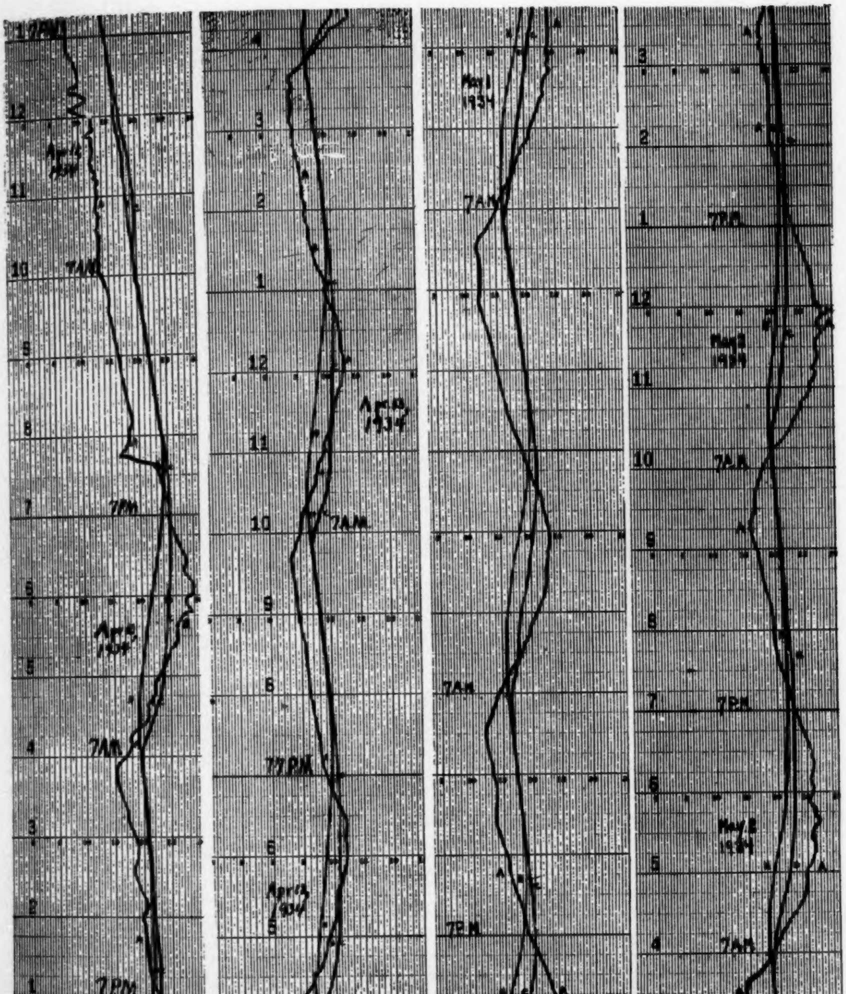
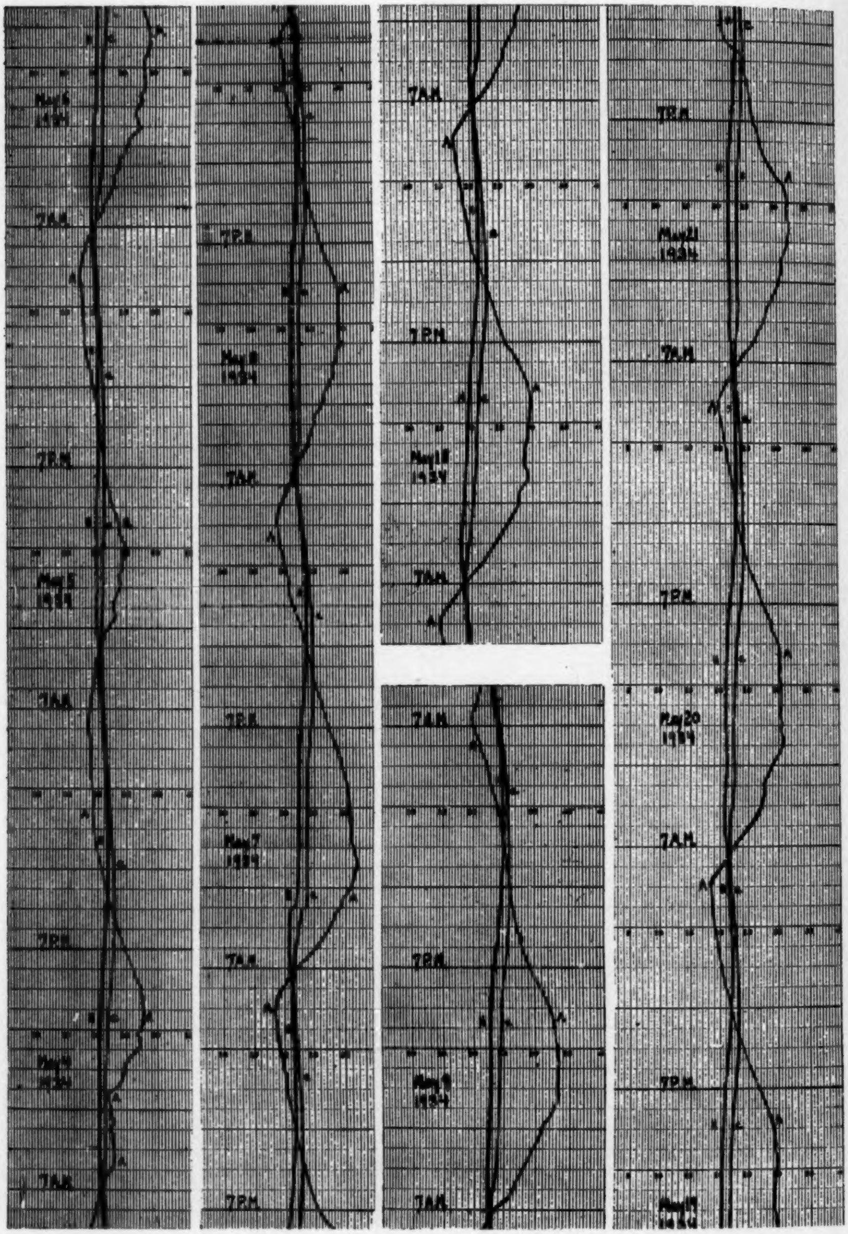
Mar. 21 1934
Apr. 3 1934
Apr. 2 1934
Apr. 1 1934
Apr. 5 1934
7 A.M.
7 P.M.

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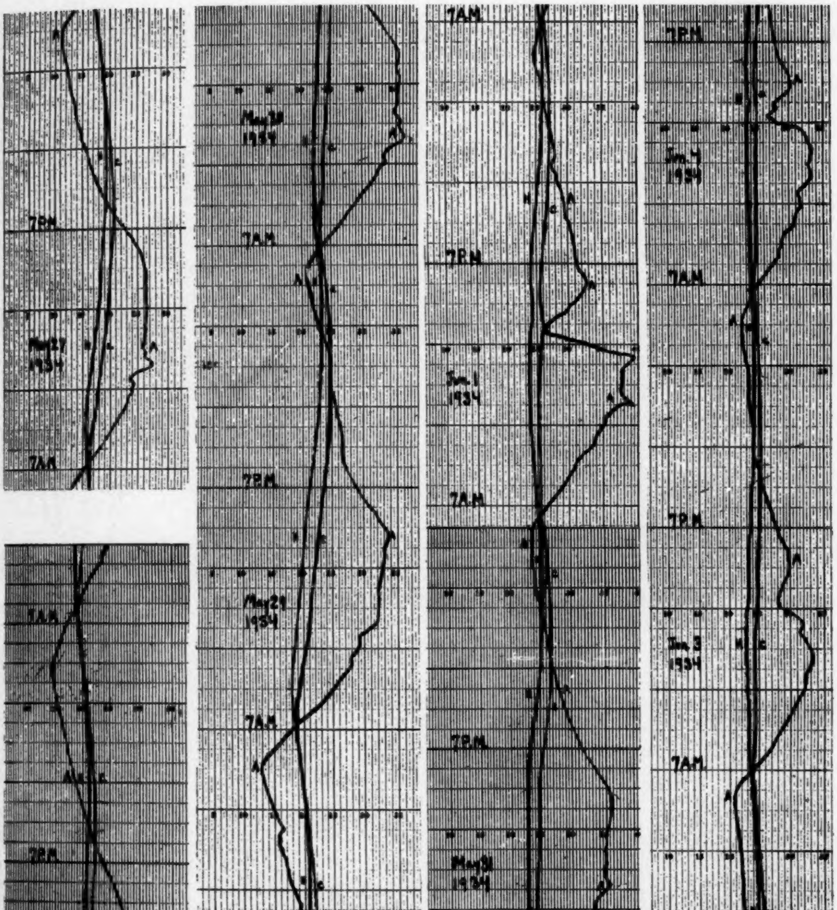
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7P.M.
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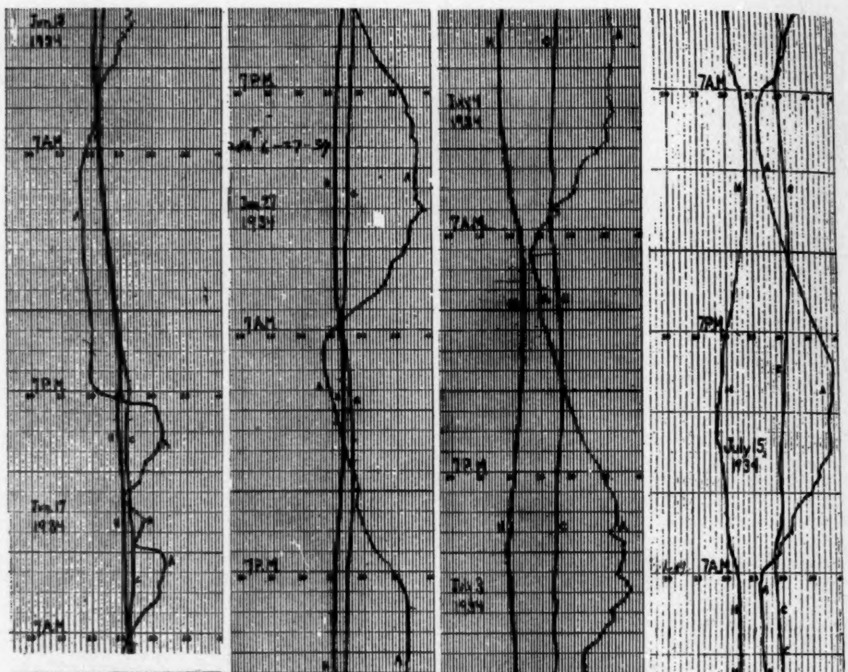
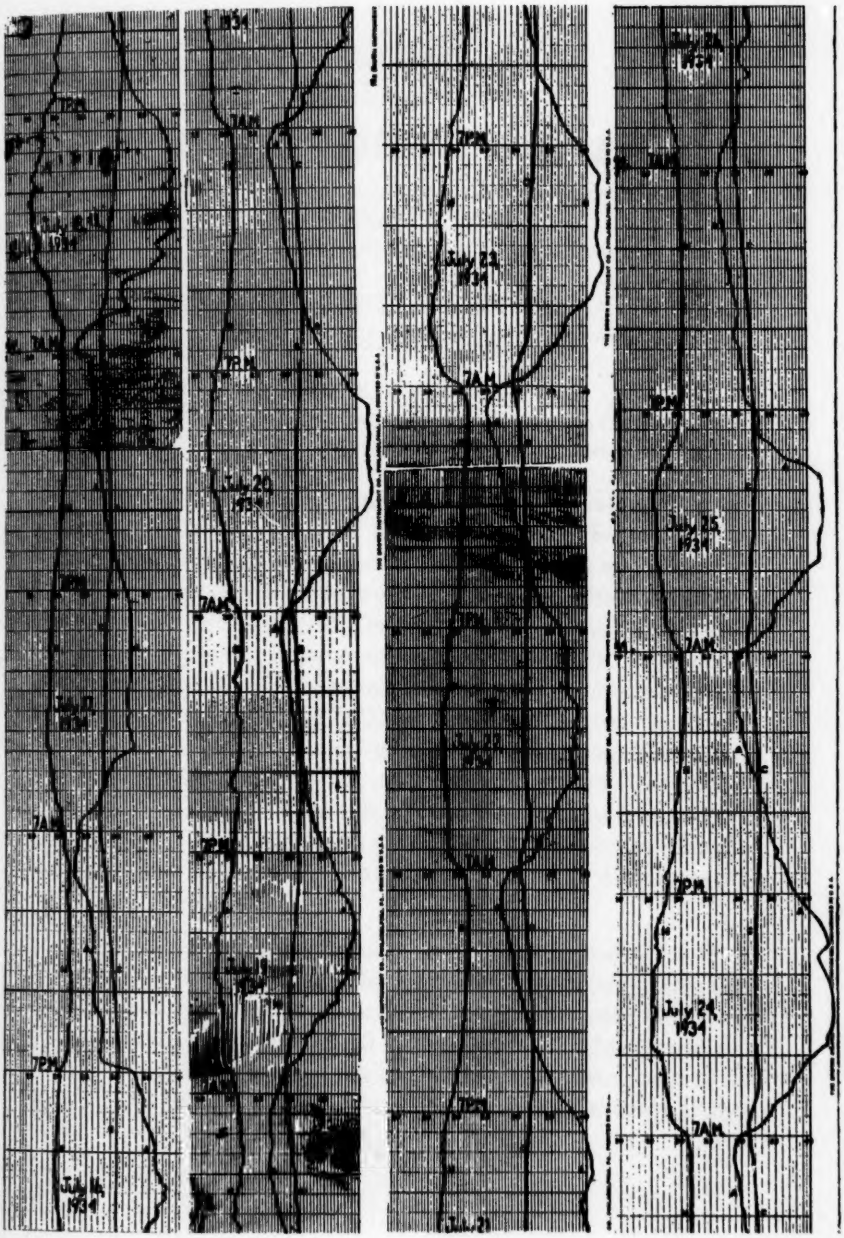
Jun. 1 1934
May 31 1934
Jun. 4 1934
Jun. 3 1934
Jun. 2




1934
7P.M.
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July 14
1934
July 20
1934
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July 23
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July 24
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July 25
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